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THE RÔLE OF REPRODUCTION IN EVOLUTION[1]

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THE establishment of methods of reproduction which maintain variation and inheritance mechanisms on a high plane of efficiency is naturally a fundamental requirement in organic evolution. Since, however, inheritance mechanisms presumably equivalent are common to every method of reproduction, one should be able to interpret the evolutionary tendencies in the matter by comparing their effectiveness in offering selective agencies their raw material. Some will hold this statement to be a self-evident truth; others may maintain as strongly either that the premises are wrong or that the conclusion is not justified even if the premises be granted. Perhaps it is safer to ply the middle course; if the case is not so obvious as a Euclidian axiom, as a compensation rigorous proof may be less difficult.

As a basis for argument, let us sketch the general trend of reproductive evolution in plants and animals.

Ordinarily, one speaks of two types of reproduction among organisms, asexual and sexual. This is a convention that has taken on the dignity of a "folkway" among biologists. Its employment should imply assent to the proposition that the varied forms in which each of these classes presents itself are inherently equivalent, and that

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the groups considered as units are fundamentally distinct, but it is doubtful whether any such implication would be admitted by the majority of its users. In fact one could hardly maintain that simple division, sporification, the production of gemmules, true budding, fragmentation with regeneration of parts, and the various kinds of apogamy and parthenogenesis on the one hand, and all nuclear fusions on the other, can be grouped together as if they are of the same evolutionary value, if this term be used in any narrow or special sense; but from a broader viewpoint, the conventional classification has a real and deep meaning which perhaps the biologist has grasped instinctively.

There are both asexual and sexual methods of reproduction in nearly all groups of animals and plants; among animals the second has almost supplanted the first, among plants the two have continued side by side. In neither kingdom was sex developed as a more rapid means of multiplication, since, as Maupas showed, a single infusorian may become the progenitor of some 50,000 individuals during the time necessary for one pair to conjugate. Some other requirement was fulfilled; and fulfilled adequately if we may judge by the number of times sexual differentiation arose and the tenacity with which it was retained.

Just when sexual reproduction first originated in the vegetable kingdom is still a question. Among the lower forms only the schizophytes, flagellates and myxomycetes have passed it by. Perhaps it is for this reason that these forms have remained the submerged tenth of the plant world. It is tempting, as Coulter (1914) says, to see sex origin in the Green Algæ. There, in certain species, of which *Ulothrix* is a good example, spores of different sizes are produced. Those largest in size germinate immediately under favorable conditions and produce new individuals. Those smaller in size also germinate and produce new individuals, but these are small and their growth slow. Only the smallest are incapable of

carrying on their vegetative functions. These come together in pairs. Two individuals become one as a prerequisite to renewed vigor. Vegetative spores become gametes. Something valuable—speed of multiplication—is given up for a time that something more valuable in the general scheme of evolution may be attained.

This is indeed an alluring genesis of sex. Let us use the indefinite article, however; no doubt it is *a* genesis of sex, but it can hardly be *the* genesis of sex. Various manifestations of sex are present in other widely separated groups of unicellular plants, the Peridineæ, the Conjugatæ and the Diotomeæ—the Conjugatæ being indeed the only great group of plants in which there is no asexual reproduction. In these forms one can not make out such a good case of actual gametic origin, but the circumstantial evidence of sex development in parallel lines is witness of its paramount importance.

After the origin of sex, many changes in reproductive mechanisms occurred in plants, but almost all of them resulted merely in greater protection of the gametes, in increased assurance of fertilization, or in provision for better distribution. First there was a visible morphological differentiation of gametes, the one becoming a large inactive cell stored with food, the other becoming small and mobile. Then came the evolution of various sex organs, and finally the alternation of generations. In the higher plants a long line of changes have occurred connected with the alternation of generations; the spore-producing type has developed from a form of little importance to that which dominates the vegetable world, the gamete-producing type has degenerated until it consists of but two or three cell divisions. In these variations there is reproductive insurance, something which also may be said of those manifold adaptations which provide zygotic protection either in the seed or the adult plant, but they are no more direct changes in reproductive mechanism than are the diverse means which arose to secure dispersal. In fact in all of these changes no new

process of fundamental evolutionary significance occurred, unless it be the various mechanisms devised to promote or to insure cross-fertilization, and which may be interpreted as variations tending to perfect sexuality.

Coincident with the general trend of plant evolution just mentioned, two important changes in the nature of retrogressions occurred, which have persisted in many species. A new type of asexual propagation arose, apogamy, which though it appeared under several guises, apogamy in the narrow sense, parthenogenesis and polyembryony, is none the less asexual reproduction returned under another name and apparently with no particular advantages over the older types. Further, hermaphroditism was developed and has persisted in numerous lines. We may be wrong in calling hermaphroditism a retrogression, for it has the great advantage of a certain economy of effort in the production of gametes, but nevertheless it is certainly a change which *per se* is in the opposite direction from that established when sex was first evolved. A moment of consideration not only makes this clear, but gives us a pretty satisfactory proof that the gain made when continuous multiplication was halted for a time by the intervention of a fusion at the genesis of sexual reproduction was in some way connected with the mixture of dissimilar germplasms. This conclusion is hardly avoidable from the fact that although hermaphroditism retained the cell fusion mechanism of gonochorism it was still necessary for Nature to evolve means for cross-fertilization. And the multitude of ways in which she solved this problem must mean that an immense advantage was secured.

In spite of the great morphological differences between animals and plants, the essential evolutionary changes affecting reproduction in the two kingdoms have been so similar as to be almost uncanny. Accepting the division of animals into twelve phyla as recognized by many modern zoologists (Parker and Haswell), one finds the following facts regarding reproduction. Asexual repro-

duction in the narrow sense is common in Protozoa, Porifera, Cœlenterata and Platyhelminthes, and is sporadic in Molluscoida, Annulata, Arthropoda and Chordata. If fragmentation and regeneration be included, Echinodermata and possibly Nemathelminthes are added. If parthenogenesis is included, Trochelminthes is admitted. Thus only the Mollusca have no form of asexual reproduction, and zoologists would hardly feel safe in maintaining its absence there since the life history of so many forms is unknown. This being the case, one must admit that asexual reproduction has been found satisfactory for most of the great groups of animals as far as actual multiplication is concerned. For other reasons, however, it evidently did not fulfill all requirements, since sexual reproduction is established in every phylum. Further, omitting the Protozoa in which it is difficult to decide such sexual differences, gonochorism is present everywhere except in the Porifera, and hermaphroditism everywhere except in the Trochelminthes, although in Nemathelminthes, Echinodermata and Arthropoda it is rare.

Now if our conclusions regarding the true rôle played by sex in evolution are correct, hermaphroditism is a secondary and not a primitive phenomenon. In this we follow Delage, Montgomery and Caullery rather than the majority of zoologists. We believe it to be the only logical view in spite of the fact that the Porifera, usually considered so unspecialized, are all hermaphroditic. Perhaps the Porifera are farther along in specialization than is admitted, for to find the substance nearest chemically to the so-called skeleton of the sponges one must turn to the arthropods (the product of the spinning glands of certain insects). Hermaphroditism, therefore, as in plants, is from this viewpoint a regression. And as in plants it was not found adequate. In giving up diecism for monecism, something was lost, and this something had to be regained by further specialization. Hence, even as in the vegetable kingdom one finds the essential feature of bisexuality, mechanisms providing for mixtures of dif-

ferent germplasms, restored by means of protandry, protogyny or self-sterility.

In even such a brief consideration of the more important changes which have occurred in the reproductive mechanisms of animals and plants, one thing stands out impressively. Both animals and plants have adopted as the most acceptable and satisfactory modes of reproduction, methods which are identical in what we deem to be the essential features, something that can be said of no other life process. These significant features are the preparation of cells which in general contain but half of the nuclear material possessed by the cells from which they arise, which are differentiated into two general classes that show attraction toward each other, and which will fuse together in pairs to form the starting point of a new organism. This parallel evolution is of itself valid evidence of the importance of the process. Let us return to our original proposition for its interpretation.

First, is there any evidence that sexual reproduction differs from asexual reproduction in what may be called the heredity coefficient? In other words, does one method hold any advantage over the other as an actual means for the transmission of characters? I have answered this question in the negative, but it must be confessed that the basis for this answer is a long and intimate experience in handling pedigree cultures of plants rather than the study of a large amount of quantitative data bearing directly on the problem. Quantitative data are to be found, of course, and plants furnish the best material because of the ease in handling large numbers of both clons and seedlings side by side; but even with the best of plant material, several undesired variables are present. Practically the inquiry must take the form of a comparison between the variability of a homozygous race when propagated by seeds and when propagated by some asexual method. The first difficulty is that of obtaining a homozygous race and thus eliminating Mendelian recombination. The traditionally greater variability of seed-propagated

strains is due wholly to this difficulty, I believe. It may be impossible to obtain a race homozygous in all factors. There may be a physiological limit to homozygosis even in hermaphroditic plants. The best one can do is to use a species which is naturally self-fertilized, relying on continued self-fertilization for the elimination of all the heterozygous characters possible. I have examined many populations of this character in the genus *Nicotiana* and have been astounded at the extremely narrow variability they exhibit. Even though one can not grow each member of such a population under identical conditions as to nutrition, the plants impress one as if each had been cut out with the same die. Qualitative characters such as color show no greater variation, as far as human vision may determine, than descendants of the same mother plant propagated by cuttings. Further, in certain characters affected but slightly by external conditions, such as flower size, the sexually produced population not only shows no greater variability than the asexually produced population, but it shows no more than is displayed by a single plant. Yet one must remember that in such a test the seeds necessarily contain but a small quantity of nutrients, and for this reason the individual plants are produced under somewhat more varied conditions than those resulting from cuttings, hence it would not have been unreasonable to have predicted a slightly greater variability for the sexually produced population even though the coefficient of heredity of both were the same.

I have made similar though less systematic observations on wheat—an autogamous plant almost as satisfactory for such a test as *Nicotiana*—with practically identical results. I do not know of any published data on the subject, however, taken either from these or any other plants. In fact, there are few other plants from which data could be obtained with so little likelihood of experimental error.

On the other hand, zoology has furnished a considerable amount of such evidence (*cf.* Casteel and Phillips,

1903; Kellogg, 1906; Wright, Lee and Pearson, 1907). One need only mention Kellogg's work on bees as a type. Kellogg assumed that if amphimixis were the principal cause of the continuous variations postulated by Darwin and Weismann as the most important source of material for the use of the natural selection,[2] parthenogenetically produced individuals should be less variable than those produced sexually. A statistical investigation showed, however, that the characters of drones probably are more variable than those of worker bees of the same race. Since Kellogg believes Darwin's judgment that "males vary more than females" to have been disapproved, he concludes that "amphimixis is not only not necessary in order to insure Darwinian variation, but there is no evidence (that I am aware of) to show that it increases variation."

It is hardly necessary to point out here the numerous mathematical and biological pitfalls which should be considered before one could accept as valid the statistical differences that appear to exist when coefficients of variation based on such data are examined. It should suffice to note that the researches of Wright, Lee and Pearson (1907) on wasps of the species *Vespa vulgaris* showed just as great a difference in variability between workers and drones in favor of the former. Apparently, the statistics in these two nearly related groups lead to opposite conclusions; in reality probably neither statistical difference is significant as far as the question we are discussing is concerned. The only conclusion justified by such data would seem to be that the coefficient of heredity is as high in the production of asexual as it is in the production of sexual forms.

Moreover, one can not expect anything more definite from this method of attack. Biologists may differ as to

[2] It should be noted here that all parthenogenetic eggs are not mere spores. Some preparation often occurs through the emission of one polar body. This may be merely a kind of recapitulation, a vestigial process no longer having any significance whatever, but since we are not certain it seems to the writer that the evidence from plants at present must be regarded as stronger.

the definition of fluctuation, mutation, etc., but they are generally agreed that germinal variations, be they great or small, are in most species so rare they can not be gauged by the use of ordinary statistical methods. For this reason, a comparison between the variability of the drones and of the workers of a pure race of bees is not likely to show any difference between these two modes of reproduction in the matter of the frequency or the type of the germinal variation produced, and can not answer the question as to whether sexual reproduction contributes more material for the use of natural selection than asexual reproduction. A study of variability in crossed races, where the effect of Mendelian recombination can be considered, would be a more logical attack upon the second problem, but is hardly necessary in view of the other evidence available.

One is then justified in claiming there is no experimental evidence to show that sexual reproduction in itself is not an exact equivalent of asexual reproduction in the matter of a heredity coefficient, but is this also true for germinal variation? We believe it is. Variations there are in both asexual and sexual reproduction, but it can not be maintained that they occur more frequently in the latter. There are insects in Oligocene amber apparently identical with those of to-day, proving that constancy of type is possible through long periods of time under sexual reproduction; yet germinal variations occur to-day in somewhat noteworthy numbers, as Morgan's work on *Drosophila* shows, although the proportion of these variations which show possibilities of having an evolutionary value, as evidenced by persistence in natural types, is probably small. On the other hand, the number of variations produced under the dominance of asexual reproduction can not be said to be less numerous, even among organisms of a relatively high specialization. If there are those who doubt this statement, let them refer to the immense list of bud-variations in the higher plants compiled by Cramer (1907).

There would be little reason in pushing the claims

further, since even though there does not seem to be a sufficient difference between sexual and asexual reproduction in the matter of variation frequency to make it a subject of experimental proof, certain theoretical points raise the suspicion that there is such a difference. All we would maintain is that to account for the general persistence of sexual reproduction by such a cause, the difference in its favor should be so great that it could easily be determined experimentally. Since this is not true, we believe the hypothesis should be discarded.

The points of theory referred to are these. It will be allowed by all that there is some considerable evidence of the chromosomes being the most important conservators of hereditary factors—the physical bases of heredity in whatever form they may be. If it is assumed then that changes in constitution in these cell organoids are followed by changes in type, and that such changes in constitution are equally probable in all chromosomes, it follows that parthenogenetic individuals having the haploid number of chromosomes should show a larger proportion of germinal variations than members of the same species having the diploid number of chromosomes, because variations of all kinds should be recognizable in the former case, while in the latter, recessive variations could not be detected until the first or second filial generation, and then only when the proper mating was made. There is some evidence that this reasoning is not wholly improbable. But variations occur much more frequently in heterozygotes than in homozygotes. To me this simply means that bud-variations *are detected* more frequently in heterozygotes than in homozygotes: and an interpretation is not hard to find. Retrogressive variations are much more frequent than progressive variations, and a retrogressive variation in a particular character shows only when the organism is heterozygous for that character. If a retrogressive bud-variation arises in a homozygote and gametes are afterwards developed from the sporting branch it is not at all unlikely that the variation may show in the next generation, but it will be attributed then to

gametic mutation. If one compares asexual and sexual reproduction from the standpoint of frequency of variation only, then sexual reproduction may seem to hold the advantage over asexual reproduction in the usual sense; but parthenogenesis, which is certainly a form of asexual reproduction, is in theory better adapted than sexual reproduction for giving large numbers of variations.

If, therefore, one is constrained to agree that the bulk of the evidence points to a practically identical coefficient of heredity for both forms of reproduction, and that variation in the sense of actual changes in germinal constitution *may* occur with greater frequency in asexual reproduction, if there is any difference at all between the two forms, he is driven either to the conclusion of Maupas that continued asexual reproduction is impossible through some protoplasmic limitation or to the conclusion of Weismann that a mixture of germplasms offers sufficient advantages to account for everything. This is the dilemma[3] unless one wishes to maintain that efficient mechanisms for nutrition, adaptation, protection and distribution could not be evolved or maintained under asexual reproduction.

The contention of Maupas can not be dealt with experimentally any more successfully than the question as to the inheritance of acquired characters since experimental time and evolutionary time are not of the same order of magnitude. The long-continued experiments of Woodruff in which vigorous strains of paramecium have been kept dividing asexually for several thousand generations, however, as well as the botanical evidence that numerous species having no sexual means of multiplication have continued to exist during long periods of time, weight the balance against him. One need not hesitate to concede that all of these organisms are rather low unspecialized types; the modern development of genetics has built up such a solid structure in favor of Weismann's view that there is little need of argument along the older line.

[3] Naturally another hypothesis wholly new to biology may be submitted at any time.

The main argument in favor of Weismann's viewpoint does not take long to state. It is this: Mendelian heredity is a manifestation of sexual reproduction. Wherever sexual reproduction occurs, there Mendelian heredity will be found. The very fact that it describes the sexual heredity of both animals and plants is sufficient proof of its generality in this regard. Now if N variations occur in the germplasm of an asexually reproducing organism, only N types can be formed to offer raw material to selective agencies. But if N variations occur in the germplasm of a sexually reproducing organism 2^n types can be formed. The advantage is almost incalculable. Ten variations in an asexual species mean simply 10 types, 10 variations in a sexual species mean the possibility of 1,024 types. Twenty variations in the one case is again only 20 types to survive or perish in the struggle for existence; 20 variations, in the other case, may present 1,032,576 types to compete in the struggle. It is necessary to hedge the argument by pointing out that these figures are the maximum possibilities in favor of sexual reproduction. It is improbable that they ever actually occur in nature, for 2^{20} types really to be found in the wild competing for place after only 20 germinal variations would mean an enormous number of individuals even if the 20 changes had taken place in different chromosomes, and if the variations were linked at all closely in inheritance the number required would be staggering. But there are breaks in linked inheritance, and the *possibility* is as stated.

These advantages remain even though it should be shown later that the more fundamental and generalized characters of an organism are not distributed by Mendelian heredity. Loeb (1916) believes that the cytoplasm of the egg is roughly the potential embryo and that the chromosomes, distributed as required by the breeding facts of Mendelian heredity, are the machinery for impressing the finer details. There is something to be said for this point of view, though at present it is but a working hypothesis. But granting its truth it does not detract from the advantages gained by sexual reproduction. Even the most

strict mutationist would hardly maintain that evolution in general has come about through tremendous changes involving sterility between the mutant and the parent types. It seems unnecessary to deny such possibilities; but the weight of evidence is in favor of the majority of variations being comparatively small, changes in detail, the very kind which are known to be Mendelian in their inheritance.

Yet sexual reproduction in itself does not assure these advantages, though they are based upon it. There must be means for the mixture of germplasms. This opportunity was furnished originally by bisexuality. Then came hermaphroditism, manifestly an economic gain, yet on the whole unsuccessful except as functional bisexuality was restored by self-sterility, protandry, protogyny or mechanical devices which promoted cross-fertilization.

The prime reason for the success of sexual reproduction then, as Weismann maintained, is the opportunity it gives for mingling germplasms of different constitution and thereby furnishing many times the raw material to selective agencies that could possibly be produced through asexual reproduction. Further, there are three minor advantages which rest upon the same mechanism. They are minor advantages only when compared to the major, and should not be passed by.

Let us first consider heterosis, the vigor which accompanies hybridization. This phenomenon has long been known. It is characteristic of first generation hybrids both in the animal and vegetable kingdoms. It affects the characters of organisms in much the same manner as do the best environmental conditions. In other words, the majority of characters seem to reach the highest development in the first hybrid generation. The hybrid individual therefore holds some considerable superiority over the individuals of the pure races which entered into it, and is thereby the better enabled to survive and to produce the multiplicity of forms which its heterozygous factors make possible. The frequence of this phenomenon, for it is almost universal, together with the fact

that it seems impossible to fix the condition, led Shull and the writer independently to the conclusion that certain factors in addition to their functions as transmitters of hereditary characters also had the faculty of carrying some sort of a developmental stimulus when in the heterozygous condition. The recent work of Morgan on linked characters, however, makes it possible to give another interpretation, as Jones (1917) has demonstrated. If it be assumed that several variations have occurred in each of one or more chromosomes, then it can be shown that the first-generation hybrid between such a variant and the race from which it arose will bring together all dominant or partially dominant characters. In the second hybrid generation, on the other hand, Mendelian recombination steps in and makes it improbable that many individuals shall have such a zygotic composition. And only in the rare cases where the proper breaks in linkage have occurred can a homozygous individual of this type be produced.

The latter hypothesis holds the advantage that it furnishes hope for a homozygous combination as valuable as that of the first hybrid generation no matter how rarely it may be assumed to occur, but whether it holds for the majority of organisms or not may depend on a future decision as to the frequency of side-by-side synapsis as compared to end-to-end synapsis. Our knowledge of linkage rests almost entirely on Morgan's work on *Drosophila* where side-by-side synapsis occurs at the maturation of the germ cells. If the break in linkage between groups of characters apparently carried by a single chromosome, which Morgan finds to be so exact in *Drosophila,* should actually depend on Jannsen's theory of chromosome, twisting at synapsis, then some other type of inheritance may be found in species having end-to-end synapsis. Perhaps this is the reason why the Œnotheras have such a peculiar heredity, for in them Davis (1909) thinks end-to-end synapsis prevails. But, be this as it may, the vigor of first generation hybrids is a fact and not a theory, and the advantage it brings to the hetero-

zygotic individual in competition with its fellows can not be gainsaid.

The investigations of Shull and of the writer on the effects of cross- and self-fertilization have brought to light another series of facts with a bearing on the problem under discussion. It has been shown that the apparent deterioration of cross-bred species when self-fertilized is in large measure and perhaps wholly due to the loss of hybrid vigor[4] through the formation of homozygotic Mendelian recombinations and not an effect of inbreeding *per se* because of the union of like germplasms. This is a plausible argument against Darwin's idea that continued inbreeding is abhorrent to Nature. It may even be said to be a valid reason for declining to accept Maupas's belief in the impossibility of continued asexual reproduction, for there is no very good reason for distinguishing between continued asexual propagation and continued self-fertilization. Inbreeding simply brings about the opposite effect from crossing, and we can see no reason for the comparative failure of naturally inbred types in the wild other than the lack of chances for progress. The one is the conservative manufacturer who continues the original type of his article, the other is the progressive who makes changes here and there without discouragement until the acceptable improvement is found. In fact, if this argument be overlooked, the inbred types which have persisted hold some advantages over the cross-bred types. The self-fertilized species are inherently strong and vigorous, witness tobacco and wheat. They stand or fall on their own merits. They are unable, as are cross-bred species, to cover up inherent weakness by the vigor of heterozygosis. Cross-fertilized maize has become the king of cultivated plants because of its variability, but many of our best varieties carry recessive characters very disadvantageous to the species.

The next secondary advantage of sexual reproduction is

[4] Accepting the view that the vigor of the first hybrid generation is due to dominant characters meeting makes this argument even more forcible.

the division of labor made possible by secondary sexual characters, using the term very generally and including even such differences as those which separate the egg and the sperm. It is not known just how these differences arose or by what mechanism they are transmitted. The greatest hope of reading the riddle lies in an investigation of hermaphroditic plants; for there are technical difficulties which seem to preclude their solution in animals. For example, breaks in the linkage between sex-linked characters occur only in the female in *Drosophila*, and as the sex chromosome is double in the female, it can not be determined whether the differentiation between male and female is due to the whole chromosome or not. But this ignorance does not give reason for a denial of the great advantage which sexes bearing different characters hold over sexes alike in all characters except the primary sex organs.

The only glimpse of the truth we have on these matters comes from recent work on the effect of secretions of the sex organs on secondary sexual characters. The effect of removing the sex organs and the result of transplanting them to abnormal positions in the body have shown that in vertebrates the secretions of these organs themselves activate the production of the secondary sexual characters. This does not seem to be the case in arthropods, however, so one can not say that primary sexual differentiation and secondary sexual differentiation is one and the same thing.

Finally there is a presumable advantage in gonochoristic reproduction in having sex-linked characters. We say presumable advantages, for all of the relationships between sex and sex-linked characters are not clear. The facts are these: One sex is always heterozygous for the sex determiner and the factors linked with it. Now it may very well be that there is an actual advantage in the heterozygous condition, as we have seen above. But should the so-called vigor of heterozygosis prove to be only an expression of the meeting of dominant characters, still a possible advantage accrues to this phenomenon be-

cause the mechanism contributes toward mixing of germplasms. As an example, let us take the *Drosophila* type of sex determination. There the sperm is of two kinds: the one containing the sex chromosome and its sex-linked factors, the other lacking it. The eggs are all alike, each bearing the sex chromosome. It follows then that the male *always* receives this chromosome from his *mother*, who may have received it from *either* her *father* or *mother*. Moreover, further variability may be derived from the linkage breaks which occur always in the female. This last phenomenon is hardly worthy of special mention, however, until it is shown to be typical of such reproduction.

This short reconnaissance presents the pertinent facts in the situation as they appear to the writer. A very great number of interesting things connected with reproduction during the course of evolution have not been mentioned. This is because it is felt that the essential feature of the rôle of reproduction in evolution is the persistence of mechanisms in both the animal and plant kingdoms which offer selective agencies the greatest amount of raw material. Other phenomena are wholly secondary.

LITERATURE CITED

Casteel, D. B., and Phillips, E. F. 1903. Comparative Variability of Drones and Workers of the Honey Bee. *Biol. Bull.*, 6: 18–37.

Coulter, J. M. 1914. The Evolution of Sex in Plants. Chicago, University of Chicago Press. Pp. 1–140.

Cramer, P. J. S. 1907. Kritische Übersicht der bekannten Fälle von Knospenvariation. Natuurkundige Verhandelingen van de Hollandsche Maatschappij der Wetenschappen. Derde Verzameling, Deel VI, Derde Stuk. Haarlem, De Erven Loosjes, pp. iii–xviii + 474.

Davis, B. M. 1909. Cytological Studies on *Œnothera*. I. *Ann. Bot.* 23: 551–571.

Jones, D. F. 1917. Dominance of Linked Factors as a Means of Accounting for Heterosis. *Genetics*, 2: 466–479.

Kellogg, V. L. 1906. Variation in Parthenogenetic Insects. *Science*, N. S., 24: 695–699.

Loeb, J. 1916. The Organism as a Whole. N. Y., Putnam. Pp. v–x + 379.

Wright, A., Lee, A., and Pearson, K. 1907. A Cooperative Study of Queens, Drones and Workers in *Vespa vulgaris*. *Biometrika*, 5: 407–422.

CONTINUOUS AND DISCONTINUOUS VARIATIONS AND THEIR INHERITANCE IN PEROMYSCUS. II

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IV. HEREDITY OF THE RACIAL DIFFERENCES

In view of the long-recognized correlation between certain of these subspecific characters—namely, those relating to pigmentation—and certain factors of the physical environment, the possibility has suggested itself that the characters in question might be purely "ontogenetic," *i. e.*, produced anew in each generation by the action of external physical factors. The simple experiment of transplanting mice from one habitat to another has disposed of this suggestion.

As I have more than once reported elsewhere (1915*a*, 1917, 1917*b*) entirely negative results have been reached, so far as climatic influences are concerned. Neither the transference of the desert race to Berkeley, nor the transference of both the desert and the redwood races to La Jolla have resulted in any demonstrable change, at least up to the third cage-born ("C_3") generation.

The La Jolla test is the more satisfactory of the two, since the number of animals employed is very much greater. Thus far, however, only the C_2 animals (38 *rubidus* and 96 *sonoriensis*) have been killed, measured and (in part) skinned. The C_3 generation is still kept alive for breeding purposes, but the characteristic racial differences are obvious. On comparing the skins of the palest and the darkest *rubidus*, or the palest and darkest *sonoriensis* of the C_2 generation, with the extremes among the wild grandparents, it will be seen that the range of color variation has not appreciably changed.

Not only are the larger color differences which distinguish these main races heritable, but certain lesser differences which distinguish narrowly localized sub-races have been shown to be genetic characters. In a recent paper (1917) I discussed an aberrant colony of "*rubidus*" inhabiting an isolated sand-spit fronting on the ocean.[15] The evidence for the inheritance of these peculiarities of color may now be stated somewhat more strongly than was done in that paper. Upon preparing the skins of the three C_1 members of this sub-race, born and reared at La Jolla, it was found that *all three* were of the aberrant hue.[16]

As regards differences relating to the measurable parts, certain preliminary explanations are necessary. It was early found that the cage-born mice depart from the wild type in certain rather striking respects. They are, on the average, considerably smaller than the latter, and have tails, feet and ears which are shorter not only absolutely but relatively. In extreme cases these malformations may fitly be termed deformities. Not rarely, too, the dorsal tail-stripe becomes so diffuse that definite outlines can no longer be distinguished. Measurements reveal the fact that this stripe becomes narrower, on the average, in the cage-born animals. Furthermore, the fertility of the captive generations is greatly reduced.

These abnormal characteristics resulting from captivity are manifested much more strongly by the Eureka race than by the desert one, or by the race which is native to this locality (La Jolla). In fact, my original stock of *rubidus,* consisting of over a hundred animals of the wild generation, has dwindled down to one male and six females in the C_3 generation. In contrast to this, no diffi-

[15] I there neglected to point out the analogy between this race and that described by Bangs (see Osgood, 1909, p. 121) from the island of Monomoy, Massachusetts. Castle and Phillips, as I learn from Dr. Castle, have bred this form in the laboratory and found its peculiarities to be "really genetic." Morgan's findings (1911) in respect to this question appear to have been complicated by the appearance of artificially induced abnormalities.

[16] In my earlier statement, based upon the appearance of the living animals, it was said that two of the three were exceptionally pale.

culty has been found in maintaining approximately the original numbers of the other two races, despite the sterility of a large proportion of the individuals. Here, then, we may note in passing, is another interesting racial difference of a physiological nature.

This deterioration of the stock, it must be pointed out, is progressive. Each generation probably presents more abnormalities than the preceding one. The causes of this condition are at present entirely unknown to me. Malnutrition or intoxication, resulting from pathogenic bacteria or protozoa in the alimentary canal, may be mentioned as possibilities. Many of the animals are now being reared in small open pens, where they are allowed to burrow in the ground. A preliminary test of this plan encourages us to hope that the troubles referred to may thus be avoided.

The following table presents mean values for certain characters in the C_2 generation, for the three races which are now being reared at La Jolla.

TABLE V

	Sex	No. of Cases	Body (Mm.)	Tail (Per Cent.)	Foot (Mm.)	Ear (Mm.)	Tail-Stripe (Per Cent.)
Eureka	♂	21	85.5	93.1	20.26	16.39	37.3
	♀	13	87.2	91.5	20.30	16.90	39.5
La Jolla	♂	61	87.4	79.6	19.62	17.66	30.7
	♀	43	89.4	79.1	19.56	17.74	31.1
Victorville	♂	45	85.3	75.6	18.65	16.43	25.9
	♀	49	87.0	74.8	18.81	16.90	26.2

It is plain from this table that, in respect to the four characters other than body length (tail length, foot length, ear length and tail-stripe), the three races have maintained the same relative positions in the series as formerly. When arranged with reference to tail, foot and tail-stripe, the series, as before, is: Eureka > La Jolla > Victorville. As regards ear length, the earlier arrangement likewise holds, viz.:

$$\text{La Jolla} > \begin{cases} \text{Eureka,} \\ \text{Victorville.} \end{cases}$$

Another significant fact does not appear from the foregoing table, however. The modifications of the three

races, indicated by the consistent reduction of all these values, has not affected them to an equal degree. In respect to all four of the characters (body length not here considered) the local (La Jolla) race has been least modified, while in respect to three of them (tail length, tail-stripe and ear) the Eureka race has been most modified. Thus there has been a mean reduction of 11 per cent. in the tail length of *rubidus*, 7½ per cent. in that of *sonoriensis*, and only 5 per cent. in that of *gambeli*. There is, therefore, a convergence between the Eureka and the La Jolla races, and if I had only these two under comparison, I might have been disposed to conclude that local conditions had brought about a modification of *rubidus* in the direction of *gambeli*. But the case of *sonoriensis*, which actually diverges farther from the local race in the C_2 than in the parent generation, shows that this explanation is not the correct one. These differences in the degree of modification are probably indices of the susceptibility of these three races to the malign influences of captivity, which have already been discussed. In harmony with this view is the fact that the Eureka mice are likewise far less fertile, under local conditions, than either of the other races.

V. Heredity of Individual Differences within Each Race

It has been shown that a wide range of individual variability occurs within each race in respect to just those characters by which one of these groups is distinguished from another. These major differences which distinguish one race from another have been shown to be hereditary. Is this likewise true of those minor differences which distinguish one individual from another of the same race?

This question can be answered by the well-known method of computing coefficients of parental-filial correlation—the "coefficients of heredity" of Pearson. I realize that the validity of this measure of the force of heredity has been called in question,[17] on the ground that

[17] By Pearl (1911) and Johannsen (1913), among others.

it does nothing more than reveal the presence of genetically different strains in a mixed population. This, however, is exactly what I wish to do in the present case. The fact that within a "pure line," where the phenomena of heredity should be least obscured, this coefficient is said to be zero is entirely irrelevant to the present situation. What we wish to ascertain is the degree to which, for example, long-tailed parents tend to have long-tailed offspring. Whether these differences among the parents are due to "mutations" or "fluctuating variations," whether they are due to single "unit factors" or "multiple factors" or no factors at all, are admittedly matters upon which these coefficients throw no light. Such questions must be decided upon other grounds.[18]

In computing these correlations between parents and offspring, we are restricted to characters which are independent of the absolute size of the individual.[19] Characters which fulfil these requirements fairly well are the *relative* tail length (ratio to body) and the relative width of the tail-stripe (ratio to circumference). My data show that the former is largely, and the latter almost wholly, independent of the size of the mouse.

The coefficients are given in Table VI. I have not thought it worth while to include their probable errors, since the significance of the set as a whole is indicated by the magnitude of most of the figures and by the fact that all but two out of the 24 are positive. The weighted means of these coefficients, combining the four races and two sexes, are: relative tail length, $+0.297$; tail-stripe,

[18] One objection, valid in certain cases, has been raised against the use of this coefficient. I refer to the contention that it may reveal resemblances which are due not to genetic relationship, but to environmental influences which are similar for parent and offspring, while dissimilar for distinct descent lines. If any one is disposed to raise this objection in the present case, it is sufficient to reply that all of my parent animals of a given race were trapped in the same restricted area, while all the offspring were reared in captivity under conditions which were practically identical for all.

[19] Unless size, itself, were to be taken as the character in question. The absolute length of the tail or foot, on the other hand, is not available for such computations. The progeny of long-tailed parents might have relatively long tails, which might, none the less, be absolutely short, owing to the small size of the individuals in question.

TABLE VI

	rubidus		*gambeli* (La Jolla)		*sonoriensis*	
	Tail	Tail-Stripe	Tail	Tail-Stripe	Tail	Tail-Stripe
Father-son	+0.36	+0.08	+0.15	+0.36	+0.23	+0.26
Father-daughter	+0.24	+0.27	+0.11	+0.53	+0.42	+0.17
Mother-son	+0.64	+0.57	+0.51	+0.36	+0.28	+0.26
Mother-daughter	+0.84	+0.47	−0.02	+0.51	+0.15	−0.02

+ 0.302. The average of four figures given by Pearson[20] (father-son, father-daughter, etc.) for the heredity of stature in man is + 0.335. There is thus found, in these mice, approximately the same degree of resemblance between parents and offspring, in respect to these two characters, as is found to occur in man in respect to stature.[21]

Since the heritability of these individual differences has been proven by means of correlation coefficients, the practicability of selection experiments with such characters is evident, provided that sufficient numbers of normal animals can be reared. Experiments of this nature have already been commenced by Mr. H. H. Collins and myself. The characters chosen for these tests are coat color, tail length and width of tail stripe.

VI. Hybridization

Successful hybrid matings have been made (1) between the Berkeley and the Victorville mice, (2) between the Eureka and the La Jolla mice, and (3) between the Eureka and the Victorville mice.

In the first case, moderate numbers of F_1 and F_2 animals were reared. In respect to coat color, the 25 F_1 individuals, when adult, ranged from a condition similar to that of an average Berkeley *gambeli* to a condition as pale and as yellow as that of the average *sonoriensis*. Moreover, there was here no marked tendency for the mean or intermediate condition to preponderate numerically over the extremes.

[20] 1900, p. 458.

[21] It is likely that the abnormal condition of the cage-born mice, described above, has resulted in minimizing this correlation. Some of the differences among them are doubtless due, not to heredity, but to differences in the incidence of the disturbing factor (infection?). The parents, having grown nearly or quite to maturity in the wild state, were not subjected to this influence.

Now it is of interest to note that the F_2 generation, consisting of 40 specimens, presented very nearly the same range, in respect to coat color, as did the F_1. The two dark extremes were of an almost identical shade, as were likewise the pale extremes.[22] No argument for "segregation" could be based upon this series which would not apply with equal force to the F_1 series.

Twenty F_3 mice, resulting from random matings of the F_2 animals, presented a range of variation which was actually not as great as that observed in the F_2 generation. The smaller number may perhaps be responsible for this difference.

It must be added that both of the parent races present a rather wide range of variability as regards coat color, and that series of the two overlap rather broadly in this respect. This circumstance complicates our interpretations much more in the present case than in that of the crosses between *rubidus* and *sonoriensis,* which will be considered later.

The Berkeley and Victorville races have been found to differ in only two of the characters which were subjected to careful measurement. The former race has a broader dorsal tail-stripe and slightly shorter ears. The second of these differences is a trifling one, however, and is not always evident when small series are compared. Moreover, the absolute length of the ear is largely dependent upon the size of the body.

Thus the width of the tail-stripe is the only accurately measured subspecific character which is available in considering hybrids between these two races. Table VII gives the mean value and the variability of this character in the two parent races[23] and in the F_1 and F_2 generations of hybrids.

Despite the small numbers of animals here concerned, two facts are of some interest. (1) The mean width of the tail-stripe in both generations of hybrids is very

[22] These remarks are based upon a comparison of skins, after death.

[23] The parent mice here used were cage-born animals, which, as before stated, were somewhat modified by captivity. They represent the limited stock which was reared in Berkeley during the earlier stages of the experiment.

nearly midway between the mean widths found in the parent races. (2) There is no increase in the variability

TABLE VII

	Number of Animals Measured	Mean	Standard Deviation
gambeli (Berkeley)	23	33.5	4.09
sonoriensis	38	26.5	4.57
F_1 hybrids	24	30.2	3.96
F_2 hybrids	38	29.3	3.54

of this character in the F_2 generation. Indeed, the standard deviation for the latter animals chances to be the lowest of the four values given.

It seems worth while to indicate the actual distribution frequencies of the tail-stripe measurements for these four groups of mice (Table VIII).

TABLE VIII

	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	Average
Berkeley *gambeli*					1				1	1	1		3	2	3		2	2	4	1	1	1	33.5
sonoriensis	2	2	2	3	2	4	2	2	2	4	3	2	2	1	1	2	2						26.5
F_1 hybrids		1				1		1	3	1	4	2	1	4	1	2	2				1		30.2
F_2 hybrids				1	1	1	3	3	4	2	6	2	3	3	3	4	1	1					29.3

In contrast to this case of the tail-stripe, it is interesting to note that, in respect to relative tail length, the F_2 generation shows a somewhat higher variability than the F_1 generation or than either of the parent races. But it so happens that this is a character *in which the parent races do not appreciably differ.*

In reality, it is probable that none of these differences in variability is significant, in view of the small numbers of individuals concerned. The explanation offered for certain differences between other hybrids to be discussed later—namely, that the F_1 and F_2 generations differed in the relative degree of abnormality—does not seem to apply here. The mean body length is about equal in the two generations, as well as the mean length of tail and foot.

The crosses between the Eureka and the La Jolla races have not been carried far enough to render any report upon them possible at present.

Hybridization of the Eureka with the desert mice was first accomplished nearly two years ago, and thus far 30 F_1 and 20 F_2 animals have been reared to maturity and measured. A very serious drawback has been the great infertility, under local conditions, of *rubidus* and anything having *rubidus* "blood." Still more serious is the abnormal state of a large proportion of the cage-born animals, which affects some of the very parts that we are chiefly concerned with in these crosses. Fortunately, the coat color remains nearly, or quite unaltered.

My series of 30 F_1 skins, taken as a whole, presents a condition about intermediate between that of the parent races. They exhibit, however, a wide range of variation, the darkest individuals being nearly as dark as some of the palest wild specimens of the Eureka race, while the palest individuals differ little in shade from a medium mouse of the desert race (Fig. 13).

In the F_2 generation we meet with a range which is little, if any, greater. The darkest skin[24] is somewhat darker than the darkest in the F_1 generation. On the other hand, the palest skin is scarcely as pale as the palest in the F_1. The preponderating effect is that the hybrids of the second generation, like those of the first, are *intermediates*. If these differences of coat color are conditioned at all by Mendelian "unit factors," there must be more than one pair of allelomorphs concerned. The monohybrid ratio is obviously lacking, and there is no segregation into distinguishable classes. Furthermore, it must be borne in mind that no indirect evidence for segregation can be pointed out in the F_2 generation which is not equally manifested in the F_1.

TABLE IX[24]

	No. of Animals	Body (Mm.)	Tail (Per Cent.)		Foot (Mm.)		Tail-Stripe (Per Cent.)	
		Mean	Mean	S. D.	Mean	S. D.	Mean	S. D.
rubidus (cage-born) ..	61	87.80	98.5		20.82		38.3	
sonoriensis (cage-born)	121	86.48	78.4		19.22		24.7	
F_1 hybrids.....	21	86.43	88.0	4.3	20.09	0.85	31.3	4.0
F_2 hybrids.....	20	84.70	84.3	6.9	19.45	1.12	33.6	6.5

[24] This happens to be a badly shrunken skin, which perhaps does not reveal the original color. The next darkest (shown in the photograph) is of almost exactly the same shade as the darkest F_1 skin.

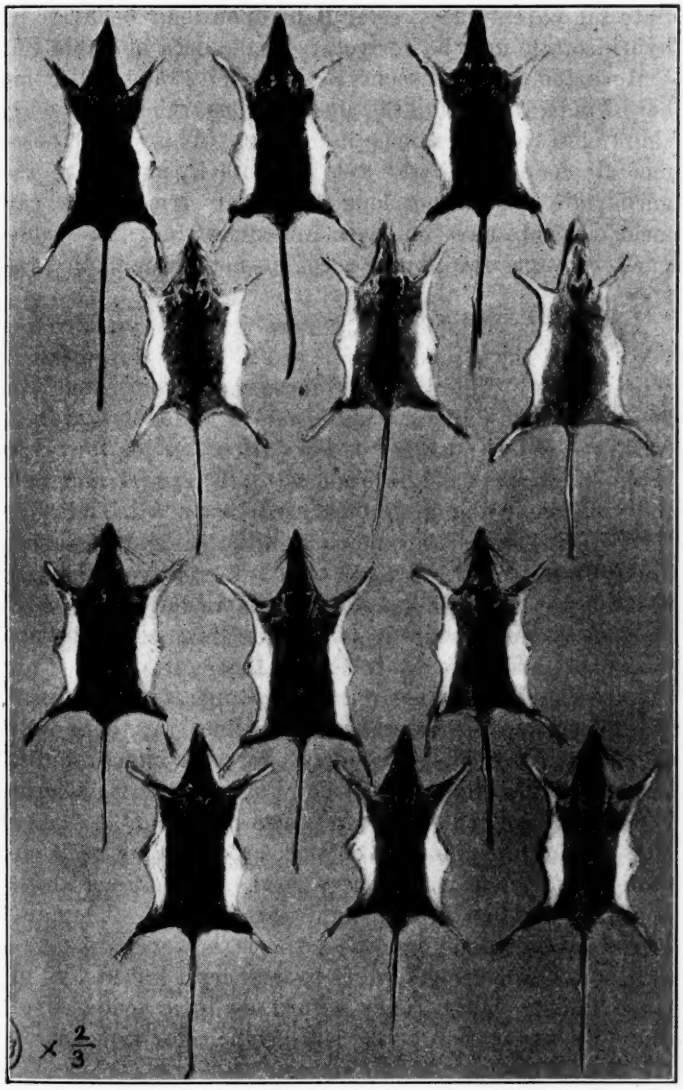

FIG. 13. Skins of pale, intermediate and dark individuals of *P. m. rubidus* (first line), of *P. m. sonoriensis* (second line), and of F_1 and F_2 hybrids between these races (third and fourth lines).

As regards the measurable characters which differentiate the parent races, some light upon their behavior in hybridization may be derived from the data in Table IX.

Here, too, one fact seems plain, despite the small number of individuals, and the modifications which these mice share with cage-born mice in general. This is the intermediate condition of the hybrids, both F_1 and F_2, as regards tail length, foot length and tail-stripe. The ear measurements have not been introduced into these comparisons, since the parent races do not differ in this respect.

As regards variability, it is seen that the standard deviations of the F_2 generation are all three larger than those of the F_1, and the differences seem great enough to be of possible statistical significance. I have, however, tabulated the frequencies of the various values for these three characters (not reproduced here), and I find that the probable explanation of this increase of variability in the F_2 generation is an increase in the amount of abnormality in the latter. This is to be inferred from the fact that the extension in range is chiefly in the direction of the *lower* values, while in two of the three cases the uppermost figures actually fall below those of the F_1. Now the abnormal influences of captivity operate by decreasing (oftentimes considerably) the values for these very characters. As further evidence for this interpretation is the fact that the average body size of the F_2 mice is here less than that of the preceding generation.

A considerable number of back crosses have been obtained between each of the hybrid combinations above discussed and one or both of the parent races. The number of individuals in any one series is, however, small, so that it is hardly worth while to deal with the results of these crosses here. They afford as little evidence of complete segregation of the subspecific color types as do the hybrids previously considered.

(*To be concluded*)

[25] Standard deviations for the parent races have been computed only for the two sexes separately. They are, therefore, not included in this table.

Nine of the 30 F_1 animals are not here included, since the *rubidus* parents of these were caught at some distance from Eureka.

INTERNAL FACTORS INFLUENCING EGG PRODUCTION IN THE RHODE ISLAND RED BREED OF DOMESTIC FOWL. III

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Winter Egg Production and the Genetic Constitution of Rhode Island Reds.—Pearl, '12, found his Barred Plymouth Rocks fell into three well-defined classes in regard to winter egg production, viz., those that did not lay at all before March 1, the zero class; those that laid less than thirty eggs with a mean at about 16 eggs, the mediocre producers; and finally those that laid over thirty eggs, the high producers. Pearl has stated, however, that the existence of the two classes of birds, mediocre and high, is the important point rather than the number of eggs at which the dividing line falls, which may be below 30 eggs in some flocks and above 30 in others. Since the record of No. 5080 is that of a typical true mediocre producer; it is clear why the division point need not fall at a particular number of eggs. If, however, the numerical record of a pullet is made the only basis for a division point, it may be pointed out that the point could be shifted by differences in environment. If, on the other hand, under the same general environment one flock was found to have a different point of division from the second flock, the latter could not be considered genetically like the first. Thus far, no satisfactory division point has been found for our Rhode Island Reds, due probably to the few records of the type shown by No. 5080 (that is, to an absence of true mediocre producers) and to the great variability in age at first egg, associated with a comparatively uniform rate of production after

the appearance of the first egg. While a true mediocre producer such as No. 5080 can easily be distinguished from a high producer in Barred Plymouth Rocks, it is impossible to draw a division line on the basis of the number of eggs produced where the egg production is of the sort observed in our Rhode Island Reds. (See Figs. 3 and 4.) Except in the case of a few individuals, the only evidence for the existence of two genetically distinct groups, such as Pearl found for Barred Plymouth Rocks, is in the shape of the left-hand portion of the curves of winter egg production. If the zero producers be omitted as a wholly artificial group (*cf.* Figs. 8 and 17) this evidence becomes less satisfactory, especially as the excess of numbers on this side of the curve may well be due to environmental factors, since the effect of such factors is almost always in the direction of decreased production. Moreover, in a later paragraph it is shown that the shape of these curves depends upon certain clearly recognized factors.

In order to eliminate any miscomprehension in regard to the characteristics of a mediocre producer, I have gone over the matter personally with Pearl. It appears that his Barred Plymouth Rocks, with the exception, of course, of the zero producers, begin to lay at about the same age, but lay at *widely differing rates.* My Rhode Island Reds, on the contrary, begin to lay at widely different ages, but lay at a fairly *uniform rate.* In the Barred Plymouth Rocks, therefore, there are three distinct *types* of winter records, zero producers, mediocre producers (Fig. 12, Nos. 274 and 284) and high producers (Fig. 3). The same types of records have appeared in a flock of Brown Leghorns which we have trap-nested.

In our Rhode Island Reds, records of the mediocre type are so rare that they must be referred either to some non-genetic origin, or a chance union of two heterozygotes, such as results in the appearance of an occasional recessive in a flock that characteristically has some domi-

nant character such as rose comb. It is quite possible that while our flock of Rhode Island Reds as a whole is homozygous for high fecundity, it is not entirely so. It is possible, of course, that many of our Rhode Island Reds are genetically true mediocre producers, but that the addition of some other genetic factor has so altered the rate of production that the records can no longer be recognized as true mediocre records.

It seems clear, then, that our Rhode Island Reds fall into the class of high producers observed in Barred Plymouth Rocks, but that the great variability in maturity results in a portion of the flock giving numerical results like those of the Barred Plymouth Rocks, but which in reality are not at all equivalent biologically. It is also clear why Castle's ('15, '16) recent criticism of Pearl's theory of egg production can not be considered to be established, in so far as it concerns *winter egg production.*

Moreover, it will be desirable in the future to distinguish clearly between the two sorts of numerical results. A discussion of the bearing of a division point at 30 eggs upon the problem is given below.

It has been maintained by Pearl that winter egg production is a satisfactory basis for selection, both for itself and as an index of the annual egg production. This would be true only when there is a definite relation between winter and annual production such as he has found for Barred Plymouth Rocks. Since winter egg production forms a part of the annual egg production with which it is to be compared, it is evident that the coefficient of correlation may be expected to have a positive value of some magnitude, unless there is a definite tendency for birds that lay well in the winter to be poor layers in the summer. On this account it has seemed best to us to compare winter production with that of the same hens for the remainder of the year. The number of birds (77) available for the comparison was not large; but the calculated coefficient ($.365 \pm .067$), while statistically significant, being six times its probable error, is too small

for use in breeding operations. While there is an evident tendency for a high winter producer to be also a high producer for the rest of the year, it seems also true, as far as the 1913–14 records are concerned—those of 1915 being at this writing incompletely worked out, though of the same general order—that there is no special tendency for birds of late start to stop early rather than late. Of course it is essential that a bird lay well in the winter if she is to make a good yearly record, and in this sense the winter egg production may be of value as a measure of fecundity, but good winter production does not insure a good annual production, nor does a low winter production necessarily mean a poor annual production. It is true, however, that birds that make the very highest records must lay throughout the entire year. From the data in hand it seems probable that winter egg production of Rhode Island Reds is not as valuable a measure of the innate fecundity capacity of a bird as it is for the Barred Plymouth Rocks.

On the average, the flocks, if grouped according to the month hatched, have an annual record that differs by an amount equal to an average winter month's production, viz., 10 eggs, as shown by Table VIII. Or, to put the matter a little differently, the average egg production of pullets hatched in March, April or May is approximately the same from February 1 to November 1. We have no evidence that the early hatched birds, on the average, stop laying earlier in the fall than those hatched later.

The influence of time of hatching on a division point at thirty eggs is very marked in the Rhode Island Reds. In Table VI the egg production of pullets laying at all during the winter is divided into an over-thirty and an under-thirty class. In the former are 68.8 per cent. of the March-hatched pullets, 58.7 per cent. of the April-hatched pullets, while of the May-hatched birds there are only 26.6 per cent. The means of the over-thirty class are 63 eggs for the February-hatched pullets, 54.9 for the March, 46.3 for the April birds, while that for the May

TABLE VIII

EGG PRODUCTION OF PULLETS HATCHED IN APRIL, MAY AND JUNE, 1915; SHOWING NUMBER OF EGGS LAID PRIOR TO AND AFTER MARCH 1, ALSO PRIOR TO AND AFTER FEBRUARY 1

	Months Hatched		
	March	April	May
Number of pullets	139	140	116
Total eggs before March 1	5,780	4,470	2,253
Total eggs after March 1 to end of year	12,951	12,974	10,982
Av. number of eggs before March 1	41.6	31.9	19.4
Av. number of eggs after March 1	93.2	92.8	94.6
Grand total	18,731	17,444	13,235
Av. yearly production	134.8	124.7	114.0
Av. number of eggs for February	10.3	12.0	11.9
Av. number of eggs before February 1	31.3	19.9	7.5
Av. number of eggs after February 1 to end of year	103.5	104.8	106.5

Note.—The data above the double bar is for birds that completed the year. A part of the data below the double bar was compiled at the end of the winter and thus includes some birds that died during the summer.

birds is 40.5. The means of the under-thirty class are 18.8 for February and for the other three months approximately 16 eggs. Now, the mean for the abstract numbers 1 to 30 is 15.5, a value which is not far from the observed mean, since the value of 18.8 eggs obtained for the February birds is probably due to the small number of individuals involved. As the value of the mean for the under-thirty birds is practically alike in all cases, and as the value of the means for the over-thirty class for the various months decreases with decreasing age, it is evident that the value, 16.1, comes mainly from the relation of the abstract numbers and has little or no significance in itself. This point will be returned to shortly.

It will be noted in Table VI that the percentage of over-thirty pullets dropped very suddenly in passing from April to May. It means, I take it, that many of the May-hatched birds did not reach a winter egg production of 30 eggs or over because of the time they were hatched. Indeed, something of this sort is to be expected when a definite number of eggs is taken for a dividing line at a particular point on the calendar. If the production curve

for May-hatched pullets be examined it will be noticed that there is a large percentage of pullets in the 16–20, 21–25, and 26–30 groups. If the average monthly production of about 10 eggs be added to these groups, most of them become over-thirty birds and the percentage of over-thirty birds becomes nearly the same as that for the April-hatched pullets. This is important, since it indicates that May-hatched Rhode Island Red pullets mature too late to furnish data comparable to Pearl's Barred Plymouth Rocks, for which it is stated (Pearl '15) that April- and May-hatched pullets alone give normal records.

Birds that begin to lay by January 1 and lay at the rate of 15 eggs per month would lay 30 eggs before March 1. This rate is about the lowest *continuous* production that has been noted, for birds that lay at a less rate usually lay intermittently. Pullets that lay at the rate specified and which begin sufficiently early in the season make very good winter records. In a recent paper Pearl, '15*b*, has remarked:

> Any bird laying 18 or more eggs per month in the months of November, December, January and February may certainly be regarded as a high winter producer.

The statement as written might imply that this rate is maintained throughout all four months, but, as this means 72 eggs and as the context implies, we take Pearl's statement to mean 18 eggs for any one month. At this rate a bird beginning to lay January 1 would lay 36 eggs before March 1. Since, however, the mode of the frequency curve of age at first egg falls at the 251–260 days group, and since the median also falls near this group, it means that nearly one half of a flock of pullets hatched May 1 will not begin to lay till after January 15, and therefore will lay less than 30 eggs. The slope of the curve indicates, moreover, that the upper limit of the range falls at about 311–320 days, which means that a few individuals begin to lay so late in life that they can not be expected to make normal records. Ten months from hatching time brings birds hatched the last of April into laying some

time in February. Three hundred and ten days seems, moreover, to mark the approximate boundary of a group of stragglers which perhaps corresponds to Pearl's after March 1 group of producers, *i. e.*, his zero producers. This group is represented in the curve by the shoulder which begins at this point, there being of course an overlap with the larger group, beginning somewhere about 280–290 days.

The relation of the *abstract* numbers involved in the series of data relating to winter egg production is a matter of some importance. The mean of the abstract numbers from 1–30 is 15.5, or from 0–30, 15, a value that corresponds closely to the mean value of the number of eggs laid by the under-thirty class. The mean value of the numbers above 30 beginning at 31 and proceeding to some other higher number such as 50 or 80, will depend in part on the value chosen for the higher number. If 80 be chosen as the higher limiting value, then the mean of the numbers 31–80 is found to have a value of 56.2. The mean values just given hold only when the abstract numbers are taken one at a time or when they are arranged in a symmetrical fashion about the mean, as, for example, in the ratio of 1:2:3:4, etc., and back to 4:3:2:1. If the 1–30 winter egg production group represented a definite genotype one would expect a symmetrical or nearly symmetrical distribution of the concrete numbers about their mean. If, however, the numbers (abstract or concrete, as the case may be) had some other sort of arrangement—as, for example, if they formed part of a normal curve of variation—a different set of mean values would be obtained, depending upon the steepness of the slope of the curve. If, for example, the classes 1–5, etc., to 25–30 inclusive, are formed and the central values appear in the ratio of 1:1.3:1.7:2:2.3:2.7, the mean will be 18.2. On the other hand, the mean of the abstract numbers above 30 that form the remainder of the normal curve, under some circumstances may shift downwards, as, for example, when the mode of the curve is at 50 with the

upper limit of the range at 90. If the observed distribution of winter egg production is mono-modal, and if its curve, base, mode and range correspond approximately to those of the curve assumed in the preceding paragraph, the mean of the numbers 1–30 will be larger than the mean (15.5) obtained from the abstract numbers in the manner chosen at the beginning of the paragraph. That is, there is a tendency for the means of the two parts of the mono-modal curve, *i. e.,* the ones derived from 1–30 and 30–90, respectively, to approach each other in value. If, however, the curve of winter egg production is a composite of two curves, *i. e.,* mediocre and high producers, then the means tend to approach those of the abstract numbers involved when distributed symmetrically.

Some doubt exists as to how our data are to be interpreted in the light of the statements in the preceding paragraph. The mean of the under-thirty group—viz., 16—while slightly higher than that of the mean for the abstract numbers—viz., 15.5—probably is not significant, though it may perhaps be taken as an indication of the existence of two genotypes. Since, however, the mean of the over-thirty group increases with increasing age and since the percentage of birds falling in the over-thirty classes increases with increasing age, it seems probable that the shape of the observed egg production curves is due to the artificial division point at March 1, while the irregularities in the curves are due to too few numbers. Since these irregularities largely disappear if the class intervals are doubled and since, if the time limits were to be extended so as to permit all birds to begin laying, it appears probable that the curve would become a symmetrical unimodal curve. Moreover, this conclusion is strengthened by the fact that the observed mean, 46.3, of the over-thirty class of the April-hatched pullets with its upper range at 77 is lower than the value (56.2) noted for the abstract numbers 31–80. For Barred Plymouth Rocks, however, the means do not rest upon the relation between the abstract numbers, but are an expression of the average production of the two types.

A comparison of the winter egg production curves obtained with the Rhode Island Reds with the similar curves for various seasons for the Barred Plymouth Rocks

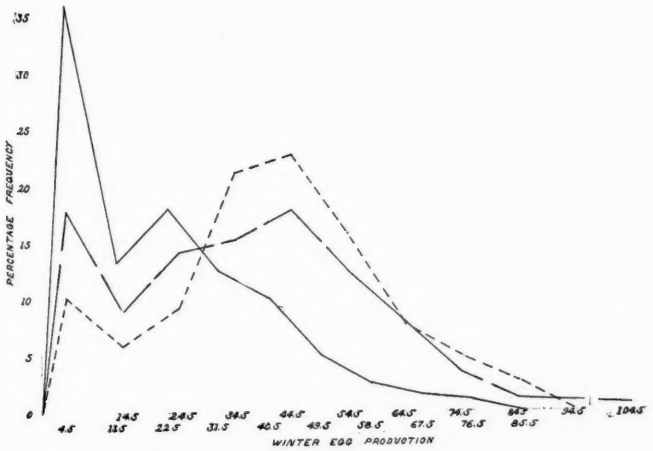

FIG. 14. Comparison of a flock of Barred Plymouth Rock pullets (Maine, 1907–08, solid line) with two flocks of Rhode Island Red pullets (Mass., 1915–16, broken line; Mass., 1913–14, dotted line) to show the difference in the shape of the winter egg production curves. For the present purpose it seemed unnecessary to regroup our data to correspond exactly to the Maine Station grouping.

brings out some interesting points. These curves are shown in Figs. 14, 15, 16 and 17. In Fig. 14 the continuous line is the frequency curve for the winter egg pro-

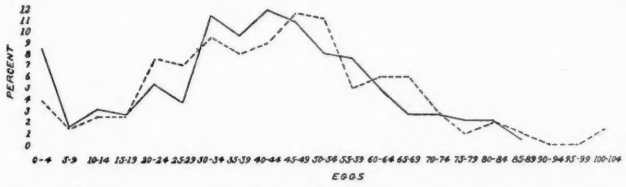

FIG. 15. Comparison of a flock of Barred Plymouth Rock pullets (Maine, 1912–13, dotted line) with a flock of Rhode Island Red pullets (Mass., 1913–14, solid line) to show the similarity in the distribution of winter egg production.

duction at the Maine Station for 1907–08, the flock reared by Pearl from the birds previously bred by Gowell for increased egg production. The line composed of short

dashes is the curve of egg production for the winter of 1913–14, made by our Rhode Island Reds hatched in March and April. This flock is the first flock about which we have full data. They were the daughters of the original flock, 1912–13, as described above, and for all essen-

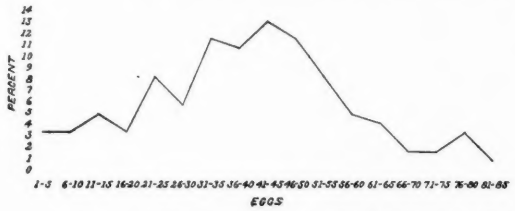

FIG. 16. Winter egg production of the Rhode Island Red pullets hatched in April, 1913. The records of these pullets have been separated from the records shown in Fig. 14 (solid line).

tial purposes were a random selection of individuals. This flock, one generation removed from its standard-bred ancestry, clearly differs from the 1907–08 flock of Pearl's in containing many more fairly high birds. The data for the 1913–14 flock, grouped in classes of 1–5 instead of 1–10,

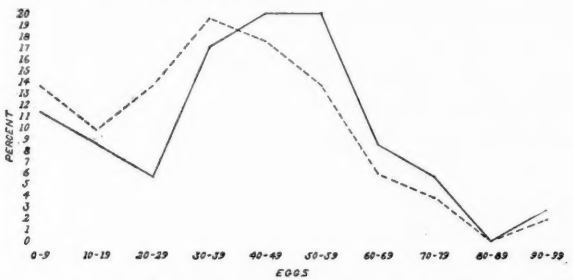

FIG. 17. Winter egg production of the flock of pullets reared in 1916 from eggs purchased of the breeder furnishing our foundation stock. The solid line represents the March hatched pullets; the broken line, the March pullets plus April hatched pullets from the same source.

is shown by the continuous line in Fig. 15, where it is to be compared with the winter record of 199 Barred Plymouth Rocks made at the Maine Station for 1912–13.[6] The essential similarity of the two curves is self-evident. As

[6] The data for the Barred Rocks was taken from Pearl (15*c*).

Pearl's pullets were (presumably) hatched in April and May, while ours were hatched in March and April, the curve for the April, 1913, hatched pullets alone is given in Fig. 16, which shows that the separation of the March pullets from the April pullets has not essentially altered the shape of the curve. The zero producers were omitted in order to study the shape of the curve when treating the zeros as an artificial group. This omission, however, would not alter the essential shape of the curve.

As already stated, new blood was added to our breeding pens in 1915. The egg production curve made by the pullets hatched in March and April for 1915–16 is shown by the broken line in Fig. 14. Compare also the separate curves for March- and April-hatched pullets shown in Fig. 8. Although some individual records better than any previously obtained were secured, on the whole egg production was not as good as for 1913–14, although still distinctly better than the production of the 1907–08 flock of Barred Plymouth Rocks.

The figures when grouped according to the month in which the birds were hatched show clearly the part played by this factor in determining the sort of records made. The curve for the March-hatched pullets is quite similar in appearance to the curve made by Pearl's Barred Rocks in 1913–14, except that the mode falls at a lower number of eggs. That is, the Barred Rocks contained a higher percentage of birds laying above 50 eggs than the March-hatched Rhode Island Reds. The curve, however, for the May-hatched Rhode Island Reds is much more like that of the 1907–08 curve of Barred Plymouth Rocks, while the curve for the April-hatched pullets is intermediate between the two.

It seemed a matter of some interest to determine whether our 1913–14 record was a chance record or whether it was a fair sample of the original stock. Consequently eggs were purchased from the original source and chicks reared in 1915. The first lot was hatched March 22 and all the pullets (39) that passed the test for

vigor were put into a laying house in October. The egg-production curve is shown by the continuous line in Fig. 17. It bears a strong resemblance to that of the Maine Station for 1912–13 and that of our flock for 1913–14. There was in addition to the 39 pullets a smaller lot hatched April 27. The curve for both lots combined is shown by the dotted line in Fig. 17. Again the curve is essentially like the 1913–14 curve for Rhode Island Reds. The writer would be glad to study the original stock in more adequate fashion, but the amount of time, labor and equipment required are so great that the end in view did not seem to warrant the expense.

Since Pearl has not discussed the question of age at first egg from the present standpoint, the possibility must not be overlooked that the factor of maturity may play an important part in his results. In a recent paper (Pearl, '16) he states that in a good laying strain the pullets mature at five or six months on the average. Quite a different state of affairs exists in our Rhode Island Reds, where the average age is much higher, about $8\frac{1}{2}$ months for the entire flock. It is clear, however, from the discussion that the factor of maturity does not influence his results to any considerable extent.

Since the two principal internal factors responsible in most cases for the number of eggs produced by a pullet during the winter are, first, the date of the first egg, and second, rate, similar sets of data may result from variability in either of the two factors. Now the date of the first egg is dependent in part on the time of year the bird is hatched, and in part on differences in maturity. The former factor is under control and can be used to eliminate differences in maturity. Rate has already been discussed in another place, but it should be noted that it may be modified by such definite factors as broodiness, or the presence or absence of cycles, as well as other physiological factors that appear to be innate but which can not be named at present. The combined effect of rate and date of first egg, or better the length of time

elapsing between the first egg and March 1, is such that the same number of eggs may result from a variation in either one of these factors. If a flock of birds all begin to lay about the same time of year, but vary greatly in the rate at which they lay, a body of data superficially the same as that produced by a flock of birds laying at a fairly uniform rate but varying greatly in the time at which they begin to lay might readily result, especially if the variability of each set of factors (rate or maturity) was very much alike. Radically different sets of data would result only if the variability belonged to quite different types. The birds that make *unusually* high winter records are those that start early and lay at a good rate throughout the winter. A poor record, on the other hand, results either from a low rate combined with a long period of production (the date of first egg coming early in the fall) or from high rate and a short period of production, since the date of first egg comes late in the winter.

A late date of beginning egg production may be the result of late hatching or of delayed maturity. That is, an early-maturing bird if hatched too late may lay no more eggs than a late-maturing bird hatched early in the spring. Thus, the actual record of a bird is the result of the influence of several factors, themselves very variable, and gives much the same result as though a much larger number of factors were involved.

Pearl has spoken of two production factors, L_1 and L_2, but has not, so far as I know, assigned either to the two chief factors concerned in winter egg production, viz., rate and age at first egg, nor does the context indicate any such sense. At first sight it might seem possible that one of these factors is a factor for early maturity, the other for rate; for according to Pearl's theory both factors must be present to secure high production, since the L_1 factor in the homozygous condition does not make a high producer. So far as can be seen, there is no objection to assigning one of Pearl's two factors to rate. Some difficulties are encountered, however, in assigning maturity

to either of Pearl's factors, for early-maturing birds almost invariably lay more than the required number of eggs even when their production is interrupted in some way. Since, however, the theory demands that both genetic factors be present for high production, the assignment of one factor to rate and the other to maturity can not be made.

THE SHAPE OF WINTER EGG PRODUCTION CURVES

The curves of winter egg production are clearly compound curves, probably belonging to the "S" type described by Pearl and Surface for monthly egg production in Barred Plymouth Rocks.

In the case of the winter egg production curves, it can be shown that this type of curve is due primarily to the variability in age at first egg, plus the date at which the census of the flock is taken. The curve, however, is modified somewhat by the variability in rate and by the fact that the birds were not all hatched at the same time. If a flock of birds were all hatched on the same day and all laid at some uniform rate, say an egg per day, it is clear that, on any given date between the date the first pullet commenced to lay and the date the last one began, the frequency polygon showing the number of eggs produced would consist of a zero class plus the remaining portion of the polygon, beginning at class 1 and proceeding through classes 2, 3, 4, etc., to the upper end of the range. Now the number of birds laying one egg apiece would depend upon the date chosen for the census and would be the number of birds that reached a given age on that date as shown by the curve of age at first egg. Thus, if Fig. 1 be taken as our standard, and some date early in the season be chosen for the census, say the date on which the flock becomes 186 days of age, the zero component of the egg curve would have a value of 99 per cent. and the 1-egg class a value of .6 per cent. At mid-season (256 days) the zero component would have an ordinal value of 55.3 per cent. and the 1-egg class a value

of 14.3 per cent., the 11-egg class a value of 9 per cent., the 21-egg class a value of 11.4 and so on. Towards the end of the season, say at 306 days, the value of the zero class would be 13.3 per cent., and the 1-egg class would have a value of 3.1 per cent., the 11-egg class a value of 5.1 per cent., the 51-egg class a value of 14.3 and so on. At the close of the season, 366 days, the zero class disappears, while each egg class has the percentage values given in Fig. 1, beginning at the extreme right and proceeding to the left, *i. e.,* the egg curve is a mirror image of the age at first egg curve.

The first modifying factor, *i. e.,* rate, tends to flatten the theoretical egg curve by shifting individuals from one side toward the other. Thus, an individual falling in the 56 class, on the 100 per cent. rate, would fall into the 36 class at a $66\frac{2}{3}$ rate. If a 50 per cent. rate were selected as the theoretical rate, the $66\frac{2}{3}$ rate hen would be shoved over into the 76 class. If the date of the first egg of a sufficiently large number of pullets all hatched on the same day were plotted on a suitable calendar, a duplicate of the age at first egg curve would be obtained; but if several hatches are grouped together, *e. g.,* the four hatches occurring in any one month, it is evident that the curve plotted on the calendar would be considerably flattened and in turn would flatten out the theoretical curve of egg production as based on age at first egg.

Selection.—Pearl's success in securing increased egg production by breeding might be due to his methods of selecting the breeders, regardless of all theoretical considerations. Families that contained all high producers were selected generation after generation to propagate the high fecundity lines. Families in which true mediocre producers appeared, *i. e.,* where segregation took place, were not used in breeding for *increased* egg production. This type of selection could hardly fail to yield results, provided that egg production is inherited. Nevertheless, it is clear that fecundity is inherited in Mendelian fashion

in Pearl's Barred Plymouth Rocks. However, the results obtained by Dryden at the Oregon Station show that individual selection in pedigreed lines as opposed to mass selection may result in improved egg production quite as well as by the application of Pearl's theory.

Egg production in the domestic fowl may seem at first sight to be a highly desirable character on which to study the influence of selection. It may be regarded as a unit character if one so desires, and if, by selection, this character is changed, it is clear that selection has been effective. But it is also clear that the effectiveness of such selection in this instance rests, in large measure, at least, upon the influence exerted by various modifying factors, such as broodiness or age at first egg, discussed in this paper. It is possible to study these factors individually both by themselves and also in their relation to egg production. Broodiness is known to behave like a Mendelian dominant, while Pearl has shown that the rate of production during the winter cycle is dependent on two genes, one sex-linked, the other a simple Mendelian character. We have found some evidence that the presence or absence of a winter cycle in fowls that lay at all during the winter[7] follows the Mendelian scheme. Since the influence of the various modifying factors is so clear cut, it is evident that egg production is a character wholly unsuited for studying the possibility of the modification of the germinal representatives of a character by selection. On the other hand, it is a good example of a character that varies continuously, but the continuity of whose variability can be shown to depend upon several modifying factors.

There is a point of some general interest regarding the genetic composition of any given flock. Hardy ('08) showed that the proportions in which a Mendelian character occurs tend to remain constant provided no selection is practised. Fanciers often practise a certain but

[7] The absence of a winter cycle in this instance means continuous production throughout the winter and spring, and *not* absence of egg production as in Pearl's Barred Plymouth Rocks.

indefinite amount of inbreeding. Under such circumstances there would be a tendency for the fecundity factors to remain in about the proportions in which they started. We may, therefore, expect to find ready-made flocks of high producers, true mediocre producers, or even zero producers as well as those containing the several types. Thus, the original Barred Plymouth Rocks of the Maine Station contained all three types, while the Cornish contain only true mediocre and zero producers.

In spite of the fact that we have *as yet* been unable to apply Pearl's theory of egg production bodily to our Rhode Island Reds (although it may yet be possible to use it after making some modifications) there is no question but that the ability to lay is inherited, as shown by a better egg production in some families than in others. It is clear also that some males produce offspring that on the whole make much better records than those from other males when the two groups of females with which they are mated are very similar in their winter egg production. In one instance, the difference between two sets of offspring by two males was clearly due to a difference in maturity. It seems clear, moreover, that some of the internal factors, such as broodiness and maturity, segregate independently.

Summary

1. The object of the present paper is to present a sur vey of the problem of egg production based on the results of four years' study of egg production in Rhode Island Reds. The presentation of the data is incidental to this object.

2. On account of disturbing factors, data from two years only is presented.

3. There are two main conclusions: First: egg production in our strain of Rhode Island Reds differs in several important respects from Pearl's strain of Barred Plymouth Rocks and also from Leghorns. Second: the egg record of a hen by itself is an unsafe basis on which

to breed for definite degrees of production, for it can be shown that egg production depends on several more or less independent internal factors and that the same number of eggs may result from the action of different sets of factors. It follows, therefore, that each factor must be studied separately, both from the physiological and genetic standpoints.

4. The factors reviewed are: date of first egg, age at first egg, growth, rhythm and rate of production, including here Pearl's genetic factors L_1 and L_2, broodiness, moult, cycles, persistence of production in the autumn, and stamina.

5. Date of first egg is shown to depend on the time of hatching, the rate of growth of the young birds and some elements, at present unknown, that determine the attainment of sexual maturity. On the average it has been found that those individuals that lay early in the fall (October) lay more winter eggs than those that begin to lay later.

6. On the average, pullets that lay relatively early (6 to 7 months) in life lay more eggs than those that lay at a later period (8, 9, or more months) in life, other things being equal. The variability in age at first egg appears to be much greater for our Rhode Island Reds than for Pearl's Barred Plymouth Rocks.

7. Birds that lay rapidly, other things being equal, lay more eggs than those that lay more slowly.

8. Some birds (true mediocre producers) lay very slowly and irregularly, producing only a few eggs (1–10 or thereabouts) per month. Others (true high producers) lay much better (15–28 eggs per month).

9. The effect of the age at which the first egg is produced on winter egg production is such that numerical results, similar to those given by true mediocre producers, may result.

10. Some pullets lay continuously or nearly so, for long periods of time. Others lay relatively rapidly, but lay in cycles with a period of rest in between. These rest

periods may or may not be associated with broodiness. In a large percentage of Rhode Island Reds, a winter cycle comparable to that found in Barred Plymouth Rocks, is absent.

11. Broodiness operates to reduce egg production very materially, for the average production is about 40 per cent. higher for the period prior to the time each individual goes broody compared with average production after that time. The apparent paradox that hens with the greatest number of broody periods lay more eggs than those with fewer broody periods is due to the fact that increased production affords opportunity for more broody periods. The presence of a large amount of broodiness in our Rhode Island Reds differentiates them from the Leghorns, which lack this characteristic.

12. The appearance of a moult often stops production. A partial summer moult was noted.

13. Other things being equal, birds that lay late in the fall lay more than those that stop early.

14. Small birds mature earlier, on the average, than large ones and hence lay more winter eggs.

15. It was observed that while birds of poor stamina might make exceptionally good records, that lack of stamina tended to delay the appearance of the first egg and hence lowered the winter records.

16. It is pointed out that while the results obtained in Rhode Island Reds differ from those obtained by Pearl in Barred Plymouth Rocks in egg production, this difference must be looked upon as a real difference just as the two races differ in color.

17. Egg production is an unsatisfactory character on which to study the possible effects of selection in modifying the germ plasm, because in reality it is complex and not a simple unit character.

18. The genetic constitution of our Rhode Island Reds in respect to Pearl's L_1 and L_2 factors has not certainly been made out, but it seems probable that as a strain they fall into Pearl's class of high producers. True mediocre producers are very uncommon in this strain.

19. The relation between the means of the abstract numbers, in the series 1–30 and 30 to some higher number, and its bearing on the use of the means of egg production of two groups falling within the same limits is discussed.

20. The curves of winter egg production are shown to be compound curves.

21. A knowledge of the factors described is of importance both from the commercial and biological standpoints. As Pearl and Surface ('08) pointed out a number of years ago, the income received from each bird will depend not only on the number of eggs produced, but also on the season at which those eggs are laid. A bird that produces 100 eggs at suitable seasons may yield as much income as a bird that produces 200 eggs at less profitable seasons.

From the biological standpoint, a knowledge of the separate factors is important because what might seem at first sight to be a simple character is really extremely complex. Obviously, then, it is necessary to attack the problem from this standpoint.

LITERATURE CITED

Castle, W. E.
1915. Some Experiments in Mass Selection. AM. NAT., Vol. XLIX.
1916. Can Selection Cause Genetic Change? AM. NAT., Vol. XLX.
Curtis, M. R.
1914. A Biometrical Study, etc. IV. Factors Influencing the Size, Shape, and Physical Constitution of Eggs. *Arch. Ent. Org.*, Bd. XXXIX.
Dryden, J.
1916. Poultry Breeding and Management. Springfield.
Goodale, H. D.
1918. Winter Cycle of Egg Production in the Rhode Island Red Breed of Domestic Fowl. *Journ. Agri. Research*, Vol. XII.
Gowell, G. M.
1902. Breeding for Egg Production. Maine Agri. Exp. Sta. Bul. 79.
1903. Breeding for Egg Production. The same, Bul. 93.
1905. Poultry Experiments. The same, Bul. 117.
1906. Poultry Experiments. The same, Bul. 130.
Hardy, G. H.
1908. Mendelian Proportions in a Mixed Population. *Science*, Vol. 28.
Pearl, R.

1912. The Mode of Inheritance of Fecundity in the Domestic Fowl. *Jour. Exp. Zool.*, Vol. 13; also Maine Agr. Exp. Sta. Bul. 205.

1915*a*. Seventeen Years Selection of a Character Showing Sex-linked Mendelian Inheritance. AM. NAT., Vol. 49.

1915*b*. Mendelian Inheritance of Fecundity in the Domestic Fowl and Average Flock Production. AM. NAT., Vol. 49.

1915*c*. Measurement of the Winter Cycle in the Egg Production of Domestic Fowl. *Jour. Agri. Research*, Vol. V.

1916. The Effect of Feeding Pituitary Substance and Corpus Luteum Substance on Egg Production and Growth. XIV.

Pearl and Surface.

1908. Poultry Notes. Maine Agri. Exp. Sta. Bul. 165.

1909. A Biometrical Study of Egg Production in the Domestic Fowl. I. Variation in Annual Egg Production. U. S. Dept. Agri. Bureau Am. Ind. Bul. 110, Pt. 1.

1911. II. Seasonal Distribution of Egg Production. The same, Part II.

Rice, J. E.

1913. Some Practical Points in the Management of Poultry for Egg Production in Poultry Culture. Bull. 1. Issued by State Board of Agriculture, Boston.

AN EXAMINATION OF THE POLICY OF RESTOCKING THE INLAND WATERS WITH FISH[1]

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THE large sums of money annually expended by both the National Government and the several states in fish propagation fall into two general fields of activity, the marine and the freshwater. The freshwater activity in turn may for convenience be divided into the production of food and game fish.

It is always proper to examine the conditions which influence restocking; and just at this time it is especially fitting to enquire into the efficacy of the methods. The technique involved in securing the eggs and their care during hatching have been well worked out. It was a marked step in advance when these modern methods were first put into practice. The money used in carrying out modern methods in the many fish hatcheries is efficiently expended so far as the writer has been able to determine. The fundamental scientific problems involved have been solved so that the regular fish foreman can successfully direct and supervise all of the steps in the process.

After the eggs have been hatched and the young fed for a certain length of time, they are distributed to the ponds and streams. The last act in the series is the one concerning which we know the least. In order to gain an insight into the actual conditions, a typical Adirondack pond was selected for study.

The whitefish is the only species that has become at all abundant as a result of the policy of the state. The fault does not seem to be connected with the number of fingerlings placed in this lake, for the state has, indeed, been

[1] Contributions from the Zoological Laboratory, Liberal Arts College, Syracuse University, C. W. Hargitt, director.

generous. The problem that confronted the writer was to discover the cause or causes for the obvious failure of this lake to support an abundance of fish after these thirty years of restocking.

In the study of the life of any given body of water or area of land, a number of fundamental relationships have

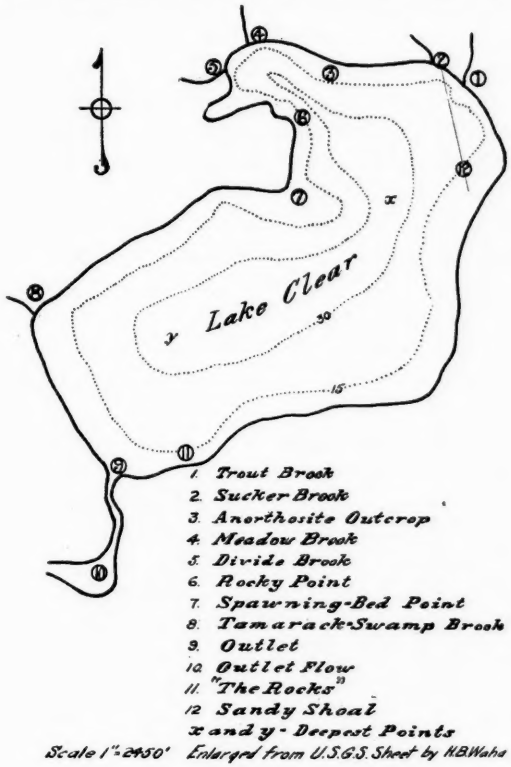


FIG. 1.

to be established before an effective detailed study can be made. After examining the conditions in several Adirondack ponds and lakes, the writer felt the necessity of examining the broader aspects of the problem with the hope that such a study might reveal some of the

causes that are influencing the present general food supply for fishes, the future food supply, the plant growth and other general problems related to the successful restocking of waters in the Adirondacks.

Such a study implies that one understand the soil and its origin. The Adirondack ponds are noteworthy for their abundance of sand. This sand is in the final analysis responsible for much of the modern life of these same ponds and lakes to-day. The geological history of the Adirondacks, especially its glaciology, is just becoming well understood by the experts. For the purposes of this paper it is simply necessary to keep in mind the fact that as the glacier receded, the Adirondacks were surrounded by a ring of ice. Within this ring of ice first the higher peaks and later the lower areas were exposed. The general result was that there were formed in succession a series of temporary glacial lakes, the remnants of which constitute the present Adirondack lakes and ponds.

Lake Clear, formerly known as Big Clear Pond, is located near Lake Clear R. R. Junction. It is at the headwater of the Saranac Lake system, so is free from the usual migration that takes place when one pond receives an outlet from another. The lake contains nearly 1,000 acres of water, which comes entirely from springs and mountain brooks. The water is clear, cool and pure—an ideal freshwater pond for restocking, one would say. What has thirty years of restocking by the state accomplished? The following table indicates that this pond has received 17,535,850 food and game fish.

In some regions, no less than eight successive lakes have been revealed by the recent critical studies of glaciologists. The net result is the accumulation of vast quantities of sand from which most of the organic food has been removed.

Lake Clear is one of the remnants of a much larger glacial lake, the shores of which are easily made out. This lake it has been proposed to call Lake St. Germain.[2]

[2] From the unpublished account of Lake Clear by Mr. Harold Alling.

FISH PLANTED IN LAKE CLEAR

	Brook Trout	Lake Trout	Rainbow Trout	Brown Trout	White Fish
1887	20,000	30,000			
1888	20,000	50,000			
1889	40,000	150,000		5,000	
1890	25,000	100,000		1,000	
1891	25,000				
1892	20,000	100,000			
1893	20,000	100,000			
1894	15,000	15,000			
1895	35,000	50,000			
1896	35,000	50,000			
1897	11,000	10,000			100,000
1898	1,600	10,000			
1899	5,000	10,000			
1900	36,000	35,000	3,000		600,000
1901	25,000				250,000
1902	750	25,000	5,000		800,000
1903	9,500	10,000	3,000		1,000,000
1904	18,000		8,000		1,000,000
1905	15,000	18,000			1,000,000
1906		50,000			1,000,000
1907	5,000	50,000			760,000
1908	138,000				800,000
1909	14,000	14,000			1,000,000
1910		20,000			178,000
1911		35,000			1,000,000
1912	10,000				1,500,000
1913	25,000	15,000			700,000
1914	55,000	25,000			1,000,000
1915	30,000	30,000			1,500,000
1916	30,000	65,000			1,500,000
	683,850	1,067,000	91,000	6,000	15,688,000

UPPER SARANAC, N. Y.,
September 30, 1916

(Signed) MILO F. OTIS

Its total area was possibly twenty times the present size of Lake Clear and included the present St. Regis lakes as well as several others. Preceding this fossil lake there was a still much larger lake more than twenty-five miles long. The station at Lake Clear and all of the level area extending north to Gabriel's Station is a small part of the floor of this large lake.

These conditions as outlined for Lake Clear in a general way apply to nearly all of the Adirondack lakes and ponds. Using Lake Clear as a center, there are in a circle, the radius of which is fifteen miles, more than seventy-five similar ponds and lakes, many of which are restocked by the state, so that the following study may

be taken as describing typical conditions in the large area of the Adirondacks.

Inasmuch as the past as expressed in the present physiography has played such a large part in influencing the present life of the lake, a brief description of the present conditions is necessary as well as the special stations at which collections were made. The names of these sta-

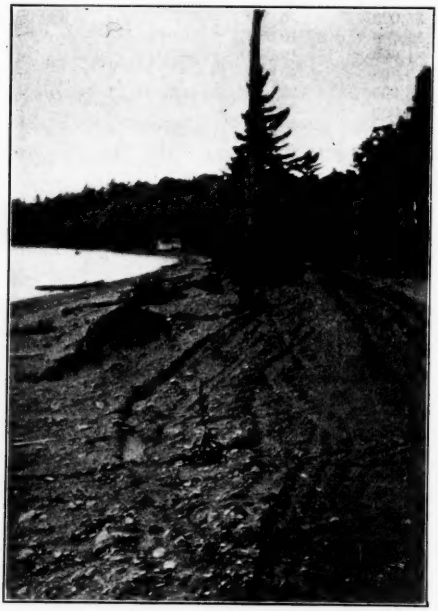


FIG. 2*a*. The shore between stations I and II. The beach is modified every spring by the ice. Note how free from vegetation this strip of the beach is clear up to the boathouse.

tions are found in Fig. 1. To these should be added the names of the two small bays, one centering at station 5, which we will name Big St. Germain Bay, and the one south of this, which we call Little St. Germain Bay.

The plant life, the ultimate source of fish food, is limited to the area between the shore and the 15-foot contour line except for the floating algal forms. This is the part of the lake, then, that is important for our study.

From just west of station 2 to half-way between stations 4 and 5, the shoal is composed of rocks and sand. The rocks are from the glacial till and similar to the soil conditions in the "fossil" shore of Lake St. Germain as exposed by the road east of the hotel. In front of Lake Clear Inn at station 3, the glacial till and sand have been washed away, leaving a small exposure of anorthosite rock. Around stations 6 and 11 large rocks and glacial till are common. The character of the soil in these three areas determines the spawning habits of at least three

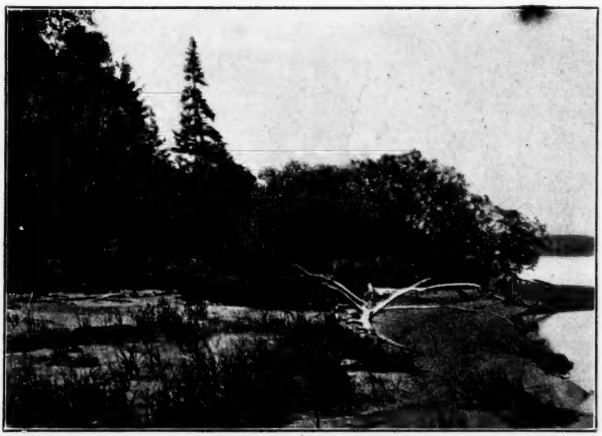


FIG. 2*b*. The shore opposite station XII.

species of fish in the lake. The remaining part of the shoal around the lake is wholly sand derived from the anorthosite rock. Station 7 is a sand point, designated as Spawning-bed Point on the oldest maps, although the frost fish are the only ones that are known to spawn there now.

The high water of early spring and the strong southwest winds cause the sand to be removed from under the trees and shrubs on the north and east shores. As the ice breaks up in May, a strong southwest wind frequently forces a large amount of ice on to the northeast shore and on the north side on to the road. On the east half of the

north shore these ice-push shores form nearly every spring, to be later washed into the lake by the heavy rains of summer. These constantly shifting shores prevent permanent vegetation, thus tending to give a barren appearance to much of the shore lines, Fig. 2*a*.

The easily modified shore extending for the most part around the six miles of shore line may be taken as a good indication of the lake bottom adjacent to it. The wave action is constantly forming sand ripples which are as constantly being changed by a heavy rain or a different

FIG. 3. Station 1, Mouth of Trout Brook. During most of the summer except after a heavy shower, the water in this stream at this place is not over six inches deep.

direction of the wind. This makes it difficult for plants to gain a foothold even if the sand were good soil for them to grow in. The general result is, then, that most of the shallow water is free from any but a very limited plant growth.

The largest brook, station 1, Fig. 3, receives several tributaries from Big Clear mountain and flows into the lake the year round. The remaining brooks, especially Sucker, Meadow and Tamarack, frequently become en-

tirely dry during August. But after a severe rainstorm all of the brooks carry a large amount of water, often more than double their normal flow, for from twelve to eighteen hours, when they return to the normal again. Thus again the large amount of sand in the soil in this region plays an important part in determining how long the water shall be retained before it runs off. After these rains the water in the lake around the mouth of the brooks is colored dark by the organic matter brought down by the water of these streams. Two important results follow: First, as this organic matter settles to the bottom, a richer soil for plant growth is furnished; and, secondly, fish tend to come to these places for their food. The amount of water flowing from Trout Brook and the frequent strong winds constantly shifting the sands prevent plants from becoming established at this place. But the water is so dark here and so much cooler that this is by all means the best place to angle for brook trout, especially by fly-casting.

The summer food of fishes has been studied by so many investigators that the main facts for the several species are fairly well understood. But the more difficult problem of determining what the available food is during the winter and what fish eat during this period is still practically unknown. One naturally thinks that all aquatic life, like the deciduous trees, perhaps, enters into a resting state for several months, but that this assumption is far from correct can be shown by the following observations.

Through the courtesy of Milo Otis, superintendent of the Saranac Inn Hatchery, I have had sent to the zoology department a large number of the so-called red hydra, each month beginning with November and ending with April. These red hydra come into the hatchery tanks through the intake pipes in Little Lake Clear. These pipes are from 30 to 40 feet below the surface of the water. The important fact is clearly established that this very simple organism, sensitive to temperature changes, lives

throughout the year and actively forms buds in January, February and March in the Adirondack waters. Microscopic sections of these hydra taken in February reveal the presence of minute Entomostracans in the enteron. Some of these minute Crustaceans taken from a jar containing the hydra were submitted to Dr. C. D. Marsh for identification. He reported that they were *Cyclops americana*. As cyclops is the common food of hydra we may assume that this species, which is very abundant, is eaten by these red hydra. At any rate, hydra feed on minute animals so that animal food is a prerequisite for their active growth.

The food of the cyclops in turn is the minute floating algal plants. These must be in relative abundance in order to support so many of the minute Entomostracans. Thus the conclusive proof of the active, reproductive habit of these red hydra throughout the winter establishes the winter active life of cyclops and unicellular algæ in Little Lake Clear.

These observations indicate a greater amount of vital activity in such cold regions as the Adirondacks than we had been led to believe existed. If these minute and simple forms of life live throughout the winter in an active state, we may safely predict that most of the other forms of life except the larger plants are also active and that the winter food of fishes is probably similar to that of the summer in many particulars.

During the summer of 1916, I had opportunity to observe the habits of the red hydra which are common in Lake Clear, particularly at station 12. A number of collections were made early in the summer and I attempted to bring some of the live animals back to the university, but in each instance the hydra died before reaching the city. I then tried to acclimate them to aquarium life, placing them in regular aquaria jars in the boathouse, but in each case the hydra died in from twenty-four to forty-eight hours after being taken from the lake. As they were kept in the lake water, the only explanation that

seems applicable is that the water became too warm for them. During these same days, hydra were coming into the hatchery troughs at Saranac Inn and reproducing in such abundance that it was necessary to clean out the troughs every three days.

In these hatchery troughs, they grow so thick that a perfect mat is formed, covering the bottom and sides in patches two or three feet long. In the center of these patches, the hydras become brown, and, if left for about a week, may become nearly white. They look as if they were dead, but when touched, contract. Hydra taken in late September in Lake Clear were all brown, with a few that were nearly white. This wide range in color is apparently due to metabolic changes taking place in the chloroplastic corpuscles.

The red hydra are a source of food for fish, for the trout in the hatchery troughs eat them after they become a few weeks old. On first hatching, the small trout are killed by these hydra. After trout fry have eaten freely of red hydra, their droppings are colored red, indicating that the chloroplasts are not broken up in digestion. Doubtless the young fish in the lake and small minnows that secure their food from the stems of plants eat many of these hydra.

A further question arises in the relation of the fish to the several physiographic conditions in the lake. This is determined by classifying the fish habitats. These are stream, barren sandy-shoal, barren stony-shoal, vegetative and deep-water.

There is no vegetation growing in the brooks except inside the bridge of Trout Brook where *Potamogeton robbinsii* and some filamentous algæ are found. At the mouth of Meadow Brook a few bullrushes and pond lilies are seen; while the Divide Brook meanders over organic débris in which a few scattering plants of *P. robbinsii,* succeed in growing. There is a narrow fringe of yellow pond lilies about twenty feet from the mouth of this latter brook, and between the shore and this fringe of lilies a

few scattered plants of the seven-angled pipewort may be seen. Ordinarily the stream habitat furnishes the most favorable ground for vegetation, yet we see in these streams a dearth of species and a limited growth that clearly indicates limited and restricted food for such animals as live upon aquatic plants.

The barren sandy-shoal, the barren stony-shoal and the deep-water habitats are each almost entirely free from plant life. This leaves the vegetative to supply the necessary food. Aside from two patches of bullrushes and two small groups of yellow lilies, the vegetative habitat is restricted to the plants that form on the slope leading to the fifteen-foot contour. At station 12, for possibly an eighth of a mile, there is a thick fringe of aquatic plants composed of *Potamogeton prealongus* and *robbinsii*. In the southeastern part of the lake and also near station 8 two other thick areas of plants occur. These consist of Potamogetons, with the addition of a third species, *P. oakesianus*. Of the possible four miles of this slope around the lake not more than one sixth supports plants.

The study of these habitats then shows that the fish are limited to the vegetative habitat in their search for such food as lives in turn upon aquatic plants.

In order to determine what the fish were actually living upon, a study of the stomach contents was made, of which the following is a summary:

Salvelinus fontinalis Mitchill. Brook Trout.—The black-striped minnow (*Leuciscus carletoni*), grasshoppers, crayfish, snail (*Campeloma decisa*), a few insect larvæ and a pumpkin seed made up the diet of the twenty stomachs examined.

Eupomotis gibbosus Linnæus. Pumpkin seed. Collected at station 8, 20 to 25 mm. long.—Daphnia and cyclops with an occasional insect larva. Fish of the same size from station 5 were feeding entirely upon daphnia and cyclops. Judging from the number found in some of these fish, I would estimate that these small fish must eat more than 1,000 crustacea daily. One specimen had

more than 100 rotifers which belonged to the species of *Hydatina.* In all, about one hundred of these small fish were studied from various stations in the lake and all were found to be eating the same food, with but a small amount of individual variation. The same is equally true of the adults of this species.

Ameiurus nebulosus Le Sueur. Common Bullhead.—The bullheads in Lake Clear vary their diet, as plant remains, crayfish, clams, snails, plumatella and daphnia are all found.

Catastomus commersonii Lacépède. Common Sucker.—Plant remains, crustacean skeletons, sand, plumatella and débris are all found.

Notropis cornutus Mitchill. Shiner.—Daphnia and insects constitute their diet. A number were found with honey bees in the stomach.

Leuciscus carletoni Kendall. Black-striped Minnow.—Insect larvæ, rotifers, algæ, plumatella and daphnia were all found.

In view of the importance of the whitefish as food fish the details of this study are given.

Coregonus clupeiformia Mitchell. Common Whitefish; Labrador Whitefish.—These whitefish are by all means the most numerous fish in the lake, as from three to four thousand are taken in the fall nets at once. More whitefish are caught than all of the other species combined, so far as my observations go. One would naturally expect, then, that more of dead whitefish would be found along the shore than of any other species. If one happened to make his observations just when the whitefish are dying, the above would be correct; but not more than two or three times during a summer are any considerable number of whitefish to be found dead upon the shores. The following notes illustrate this point.

Dead whitefish collected between September 19 and 24, 1916, just as they drifted onto the north shore between the small brooks stations 1 and 2, and the East Flats, give the daily record as follows: September 19, two males,

12½ and 8¾ inches long; September 22, 4 whitefish from shore; September 23, 5 whitefish from shore; 3 others partly eaten by crows. All of these eight fish appear to be in a healthy condition and show no evidence of starvation; September 24, 5 more whitefish from shore. The intestines of three others were taken as the body of the whitefish was already mutilated by crows. During this week a strong southwest wind blew.

On July 2 and 3 a similar series of dead whitefish was found on this same stretch of shore. A dozen fish were noted, all of which were between 12 and 15 inches in length. These had all been partly eaten by crows when first observed, so that it was impossible to learn anything about their food. The crows begin their attack upon the body in the gill region and drag out the viscera through this opening. After the visceral delicacy is eaten, the dorsal muscles are gradually removed. The crows take from two to three days to eat up a whitefish. None of these twelve fish was poor or showed any sign of starvation. A strong southwest wind had been blowing for several days.

During the past ten summers I have noticed a similar series of conditions. Two or three times each summer, a large number of whitefish are found dead on the northeast shore. Occasionally, I have noticed the skeletal remains of whitefish on the west and south shores. During these irregular times when whitefish are drifting on shore, there are more of them than suckers, bullheads, brook or lake trout. Rheighard ('13, p. 224) says:

> Great numbers of dead suckers are thrown up on the beach in South Fishtail Bay in July and August. Many of these have the characteristic form of starved fish. The back is thin and sharp instead of round, and the head is disproportionately large compared to the body. . . . The emaciated fish do not appear to be diseased and are not usually parasitized heavily enough to account for their emaciation.

Colbert ('15, p. 35) names five causes of death in fishes, as follows: (1) Mechanical injury; (2) injury through attacks of other species; (3) the beaching of individuals

while pursuing or swallowing prey; (4) the accidental beaching while attempting to escape enemies; (5) disease and parasites.

These are the two most important of the recent observations on death in fishes. The size and general healthy condition of the whitefish collected eliminate all but the first cause given by Colbert. It is well known that whitefish are easily killed by handling and do not have the tenacity of life so characteristic of suckers or bullheads, for example. The whitefish, although occupying the deep basins of the lake, frequently come to the surface to play. On a calm summer evening one can hear them as they spring out of the water. The splashes which they make are more numerous in the deep water, while the brook trout are seen in shallow water near the mouth of the brooks. This is a common habit of whitefish in Lake Clear, especially during July and August. That they come to the surface is also shown by the fact that at times many are caught with not more than six or eight feet of line. Their habit of coming to the surface makes it possible to see how wave actions might cause their death. None of the other causes cited by the observer quoted explains the death of these whitefish. In the detailed study it was found that all of the dead whitefish collected this summer were males, which renders it all the more difficult to understand how wave action may be the only cause of death.

The following study of the stomach contents of these dead whitefish throws a good deal of light upon their food habits:

No. 1. Male. Length 11¼ inches. Intestine full of food. Stomach contents badly macerated and most of it impossible to identify. Apparently almost entirely *Daphnia kahlbergensis*. No copepods. The mesentery contained a large amount of fat.

No. 2. Male. Length 11¼ inches. Stomach and intestine contain many minute crustacean skeletons. The remains of three honey bees covered with saprolegnia. A small amount of fat in mesentery.

No. 3. Male. Length 12½ inches. Stomach and intestine contain numerous minute macerated crustacea. Mesentery loaded with fat.

No. 4. Male. Length 11¾ inches. Thousands of minute macerated crustacea in stomach and anterior part of intestine. Remains of three honey bees. Small amount of fat in mesentery.

No. 5. Male. Length 12 inches. One honey bee. No fat in mesentery.

No. 6. Male. Length 11 inches. Numerous *Daphnia kahlbergensis*. No copepods.

No. 7. Male. Length 12 inches. One honey bee. Large amount of fat in mesentery and around stomach.

No. 8. Male. Length 11½ inches. Stomach empty. Intestine partly full of digested food. Large amount of fat.

No. 9. Male. Length 11 inches. Stomach contained numerous *Daphnia kahlbergensis* and *Leptodora hyalina*. No copepods. The intestine was 5 inches long and $\frac{5}{16}$ of an inch in diameter and was packed full of cladocera skeletons.

The food in numbers 1, 6, 9 were identified by Dr. C. D. Marsh. It is probable that the minute crustaceans noted in 2, 3, 4, 8 are the same as those found in 1, 6, 9. This material was so badly macerated that it was impossible to be confident of the identification.

The large amount of food found in the stomach and intestine, and the presence of a great deal of fat in most instances, is convincing evidence that these fish did not starve to death. It seems strange that they were all males. The honey bees eaten had evidently been in the water several days, as practically every one was covered with saprolegnia.

The following whitefish were collected by Milo Otis, superintendent of the Saranac Inn Hatchery. The fish were taken during November, 1916, in nets used to secure spawning fish.

No. 10. Male. Length 11 inches. Stomach empty. Duodenum contained minute crustacea, too macerated to identify. In the intestine were found numerous winter eggs of *Daphnia*. These winter eggs appear to be uninjured by the digestive enzymes. Some were found in the rectum in a perfect condition, so that I feel confident that most of them pass through the digestive canal and into the water ready to grow into *Daphnia*. This is an important fact when the problem of an adequate amount of food is taken into consideration.

No. 11. Female. Length 11½ inches. Stomach empty. Macerated cladocera in intestine. Many tapeworms present.

No. 12. Male. Length 11½ inches. Stomach empty. Intestine contains macerated cladocera. Very fat.

No. 13. Female. Length 11 inches. Stomach and intestine mostly empty. Parasites present. Ovaries full of eggs.

No. 14. Male. Length 11 inches. Stomach empty. Intestine with cladocera skeletons. Parasites present.

No. 15. Female. Length 8½ inches. Stomach and intestine empty. Cœlome full of eggs.

The following viscera taken from whitefish collected by Milo Otis were received November 24, 1916:

No. 16. Stomach empty. Several parasitic flatworms present.

No. 17. Stomach contained 3 pumpkin seeds (*Eupomotis gibbosus*) 1 inch long; 1 partly digested *gibbosus;* 1 snail (*Amnicola Limosa* Say identified by F. G. Baker). Parasitic flatworms present.

No. 18. Stomach contained many *Daphnia kahlbergensis* and *Leptodora hyalina.* No copepods.

No. 19. Stomach contained numerous *Daphnia* winter eggs; 8 whitefish eggs.

No. 20. Stomach full. One pumpkin seed (*Eupomotis egibbosus*) and 103 whitefish eggs. Parasitic flatworms present.

No. 21. Stomach empty, with many parasites.

No. 24. Stomach full of whitefish eggs.

No. 25. Stomach contained 1 partly digested fish, probably *gibbosus.*

Nos. 26, 27. Each contained many *Daphnia.*

No. 28. Stomach contained *Daphnia* and whitefish eggs.

In the jar containing the viscera of the whitefish numbers 16 to 28, there were, in addition to the above records, 20 pumpkin seeds that had been in some of these stomachs and 107 whitefish eggs. 33 tapeworms were also found in this residue.

Small pumpkinseeds were selected in order that the food habits of very young fish might be compared with the adults. Small fish 20 to 25 millimeters (about an inch), 25 to 30 millimeters, and adults 100 millimeters long (3 to 4 inches) were examined.

These young fish live almost exclusively on small cladocerans, with cyclops and daphnia predominating. Occasionally one was found having only rotifers. Insect larvæ do not play an important part in their food so far as my studies go. The adults include, in addition, plants and *Plumatella.*

Baker (1916, pp. 184–188) gives a summary of the facts of the food habits of this species in which insect larvæ and mollusca are seen to be the most important. In Walnut Lake, Wisconsin, insect larvæ are mainly eaten;

while in Douglas Lake, Michigan, and Oneida Lake, New York, molluscs are the more important. In Lake Clear, cyclops and daphnia may be said to be their main food. These two animals happen to be almost the only food of the whitefish. The pumpkin seeds in Lake Clear thus become a hindrance in the stocking of this lake. The number of pumpkin seeds eaten by other fish does not appear to be large. It is suggested that food fish which live harmoniously with whitefish but feed upon pumpkin seeds would make a valuable combination.

Forbes (pp. 108, 1883) made numerous experiments to determine the natural food of young whitefish. He found that cyclops were more important than all the other organisms combined. Hankinson (p. 239, 1914) also noted the almost exclusive diet of cyclops and daphnia. Baker (pp. 159–161) shows that not only crustacea, but molluscs are important as food for adult whitefish. My observations emphasize the limited diet of large whitefish in Lake Clear where cyclops and daphnia are all that are eaten during the summer. In the fall some specimens were taken with the snail *Amnicola* in the stomach, but this snail is present in limited numbers only, so can not be very important as a source of food in Lake Clear. During the fall, small pumpkin seeds and their own eggs are added to the daphnia-cyclops diet. It is to be noted that all of the dead whitefish were in good condition, most of them being fat. These all fed upon the daphnia-cyclops diet.

These cladocerans produce winter eggs in large numbers which are not destroyed by the digestive juices of the whitefish nor the other fish that feed upon them. These eggs pass through the entire digestive canal uninjured. This is an important factor in keeping up the number of these minute organisms. Were these winter eggs digested and used as food, it is probable that this, the most important source of food for whitefish, would soon become exhausted.

The brook trout taken in Trout Brook or at its mouth

feed for the most part on insects; while those taken in the lake eat minnows almost exclusively. The two taken early in the spring (the ice did not break up until after May first) had been feeding upon pumpkin seeds, crayfish and insect larvæ. No molluscs were found.

The food of the three species of minnows examined as well as the suckers indicates that these fish live largely on the same animals as the whitefish and the pumpkinseeds. The bullhead is the most general in its diet of any of the fish studied, taking clams, snails, crayfish, minnows and plants.

A detailed study of the food habits of the fish in any lake is necessary before one can tell just what the several species of fish actually eat. It is to be regretted that in this lake the number of organisms suitable for food for fishes is so limited. The result is that each species comes into competition with the other species for food. *The result of this competition for the one abundant food, daphnia-cyclops, prevents this lake from permanently having large numbers of food fish.*

The consideration of the history of the lake, the specific habitation of the fish, the noteworthy dearth of aquatic plants, the actual food of the fish and the restocking that has taken place during the past thirty years leads to the conclusion that restocking has not been and cannot be a success. In estimating how many fish any given body of water will support, one must first consider the variety and abundance of aquatic plants. *There can not be any more animal food for the small fish and fingerlings than can find subsistence on the aquatic plants of any given body of water.*

In this connection a second question might be asked, why stock any Adirondack pond with a distinctively food fish? Whitefish when not taken in nets are caught at baited buoys which are placed early in the spring by the local fishermen. I have counted 25 buoys scattered around the lake in early June. At these buoys a considerable number of whitefish are taken by relatively very

few people, probably not over fifteen separate families. Sportsmen who desire to fish for whitefish employ some one who has a buoy located advantageously as a guide. This guide ties the boat to his buoy. In a half day, from six to twenty whitefish may be thus taken. No one is expected to tie to one of these buoys without the "owner's" consent. The result then of this extensive stocking by the state has been to enable a few local families and guides to catch for their own use and to sell a few whitefish. The general vacation transients are not benefited nor is this excellent food fish taken in such numbers as to yield any considerable amount of food. If the state is to continue to restock such ponds as Lake Clear with whitefish, then some better method should be devised to take the whitefish.

The fundamental reason why the extensive restocking of Lake Clear has not been a success is due to the glacial origin of the lake. The mere fact that the sand in which the plants try to grow has been resorted by the glacial waters until most of the organic material, plant food, has been washed away, produces a very limited number of aquatic plants. Such plants are indispensable as a source of food for the numerous minute organisms upon which fish normally feed. One can hardly appreciate what a large number of different animals fish eat unless he has given careful study to this problem. Baker (pp. 157–199) gives a summary of the different kinds of animals eaten by fish and the variety is in striking contrast to the one abundant group of organisms (daphnia-cyclops) in Lake Clear. In order to have a general growth of fish in a lake, I believe that an abundance of *several kinds* of fish food is indispensable. The conditions in Lake Clear well illustrate how the species that can most successfully utilize the form of food that is abundant survives and greatly increases in numbers, while the others remain few in numbers.

The shores of Lake Clear are remarkably free from dead fish and one rarely finds any dead fingerlings. It

would seem as if there were but one conclusion, namely, that the most of the fingerlings are eaten by larger fish.

The probabilities are that there would not, then, have been any more trout in Lake Clear, even if the state had placed many more than it has during the past thirty years. This lake really illustrates an instance of overstocking simply because there was not an adequate amount and variety of food. At present there does not seem to be any way to remedy this deficiency.

During the past summer the states have been urged to increase greatly their production of food and game fish. This very general recommendation fails to recognize certain fundamental facts. The next step in advance along fish propagation is one that will have to be taken slowly, as it necessitates a great deal of critical information. It is becoming more and more apparent that we must not only know the breeding habits of the small minnows, pumpkin seeds, etc., the fry of which serve as admirable food for the food-fish fingerlings, but also the natural history of all of the life of a given body of water. It is a well-recognized biological axiom that no organism can live unto itself alone. This applied to our problem means that a clear and adequate supply of water is not the only factor that must be considered in deciding to restock great bodies of water with fish-fry. But rather the intricate and more or less obscure conditions that determine the sum total of life in each body of water must be taken into consideration. Such studies alone furnish a correct basis for determining the extent to which an animal may draw upon a given source of food, upon the available body of food, and many kindred problems. Before the state can wisely undertake to place more fingerlings in the ponds, it ought to know whether there is enough available food to keep them at least from starving.

The extensive restocking of most of the Adirondack ponds is done mostly for the benefit of the sportsmen. The benefit that has accrued to these and many other vacationists is very great, but one can not help wondering

if this policy should not be restricted and adjusted. One or two trout hatcheries would probably be able to produce all of the trout needed, while the rest might be turned over to the production of food fish which should be placed in the larger bodies of water that support an abundant aquatic plant life. The conditions in Oneida Lake are in such striking contrast to those in the Adirondacks that one can unhesitatingly suggest that this lake could support an incredible number of fish.

Intimately associated with this general problem is the question of disease in fishes. Under this heading are included the several forms of parasitism. Reference will be made to two or three only. This is the field in which the greatest progress has been made in the cure and prevention of the diseases affecting man. But before *prevention can be applied, the life history of the parasite must be understood.* In the main, the work of the national and state governments has been confined solely to hatchery problems. Here is a field that they should enter, as many of the problems are too large and involve too much expense for the individual.

Salmincola edwardsii (Olsson).

This parasite belongs to the copepod group of crustaceans, many of which are familiarly known as "fish-lice." Wilson says: "This family (Lernæopodidæ) of parasites is widely distributed amongst fishes in both salt and fresh water. Some of our best food and game fish are infested with them, and when they once obtain entrance to a stock pond, fish hatchery, or aquarium they usually multiply so rapidly as to become a serious nuisance, and may even kill the fish" (p. 569). There are some one hundred and thirty-six different species of animals that belong to this family, all of which are paraistic during their adult life. In the genus to which our specimens belong, there are twenty species, eighteen of which live exclusively upon the several kinds of trout.

Salmincola edwardsii is found exclusively infesting the brook trout (*Salvelinus fontinalis*). All of the specimens

taken in Lake Clear were attached to either the dorsal or anal fin. The gills of these fish were examined but no fish-lice noticed upon them. This seems strange as Fasten (1911–12) reports them as especially abundant upon the gills. They were found on trout ranging from four inches in length to those fourteen inches long, which were caught in Trout Brook, in the lake near the mouth of this inlet, station 1, and in the bay near station 5. They were taken upon both large and small fish in each of these locations. My specimens were collected during July, August and September. The last specimens were on a nine-inch male caught in Big St. Germain Bay, September 28, 1916. The egg-sacs were full of embryos.

This common "fish-louse" is easily recognized. From the main part of the body two large egg-sacs are suspended. With an ordinary hand lens, the numerous small embryos can be noted, and the small beak which attaches the parasite to its host. Fasten has recently worked out the life history and the habits of this interesting parasite, which undergoes an extensive degeneration after becoming parasitic.

These parasites are widespread in the United States in the native trout streams, and in Canada and Europe. The first scientific record of this particular parasite is by Linnæus in 1761. It seems strange that an animal could be known for so long and its habits not be understood until within the past five years. The fact that it is so widespread and has been known for so long indicates that it is not a serious pest except under very favorable living conditions. These are best found in the hatcheries or stock ponds, where many fish live in a small enclosure. The numerous parasitic larvæ then have little trouble in finding a host. In the streams and ponds of this state, we need not fear that the trout will be killed by them. The chief reason is that the trout are few in numbers in any given place, so that when the embryo parasites make their escape, there is small chance of their ever becoming attached to a trout. The result is that each trout in a

wild state does not usually harbor more than a half dozen, and this number does no serious harm to the trout, especially where they are attached to the fins.

When this pest gets into a hatchery, but little can be done. The infested trout at the Wild Rose Hatchery in Wisconsin were treated with "solutions of copper sulphate, potassium chlorate, sodium chloride, and mixtures of sodium chloride and potassium chlorate, but these had no effect upon the parasite" (Fasten, 1911–12, p. 17). About the only remedy that is effective is to destroy all of the parasitized trout, which can be done after the spawning season; for there is no reason to believe that these parasites can be carried from one place to another except in the manner described by Fasten. We do not know how these parasites pass the winter, but in view of the fact that they are not known to eat during their free-swimming period, it is probable that those which live through the winter do so as parasites upon trout. During the cold weather the growth changes would not take place as rapidly, so that a given parasite might remain on a trout for five or even six months during the winter.

Clinostomum marginatum.

This is a small Trematode that lives for a part of its life embedded in the muscles of several food and game fish. The popular name of "grubby" is used to describe this condition. So little is known about this parasite that renders thousands of dollars worth of fish unsuitable for food that any new facts are welcome. In this connection, the following field observations are recorded upon this very annoying parasite. In an earlier paper (Smallwood, '14) attention was called to the fact that these worms may voluntarily leave the body of their host after the host dies. On May 28, 1914, about 50 perch were taken from McCauley Pond between Saranac Lake village and Lake Clear Junction. After returning to camp, it was noticed that these perch were "grubby" and they were all left in a pile on the ground. The next morning, I examined the pile of perch and was able to pick up more than 100 flat-

worms that had crawled out of their cyst during the night. If I had cared to do so I could have gathered several hundred specimens during the day as they continued to escape from the cysts.

This observation answers one question, namely, that these parasitic worms remain in the body of the perch all winter, as the worms were in the same stage of maturity as those taken in July, August and September. It further suggests, also, that *Clinostomum marginatum* may return to an aquatic habit directly from the body of the fish.

Guides and fishermen claim that perch are free from "grubs" at certain seasons of the year, a belief which I am unable to confirm. But if more extended studies show that their belief is true, the method by means of which the "grubs" leave the fish has been found.

So far as we know, these parasites are mainly confined to members of the bass and perch families, although a few cases are on record of trout being infested with them. Occasionally one finds a few bullheads that are "grubby." In Lake Clear *Lepomis gibbosus* and the minnows are largely infested by them.

I can also confirm my observations (p. 11, '14) that fish eating parasitized minnows are not themselves infected through this avenue. One brook trout was found with a partly digested minnow in its stomach. In the flesh of the minnow a dead parasitic clinostomum was observed.

I would say that the number of fish harboring this parasite in Lake Clear is on the increase.

The following observations upon some larval stages in Trematodes may help to start some one upon this problem without losing a season experimenting.

During the past three years, I have frequently found in the muscles of perch and pumpkin seeds minute cysts. Each of these cysts contains a larval Trematode.

The wall of the cyst is tough and easily "shells out" of the muscles, but is not readily penetrated by the ordi-

nary killing fluids. This has resulted in my not being able to secure suitable sections for detailed study. It will probably be necessary to make most of the observations upon living material, which will require that one have a microscope and microscopic reagents while doing field work.

The following general facts may help to direct attention to this important stage in the development of the life history of Trematodes. Possibly some fish containing them may be found near a laboratory and thus readily studied.

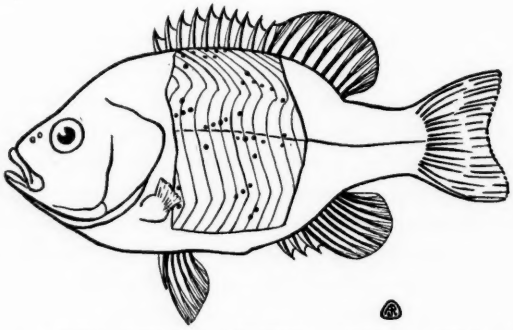


FIG. 4. *Lepomis megalotis* (Rafinesque), long-eared sunfish. Taken in Lake Clear, 1915. A portion of the skin has been removed to show the position that the larval stages of certain undetermined Distomes occupy in the flesh.

Fig. 4 shows the usual position of these larval stages in the muscles of the long-eared pumpkin seed taken in Lake Clear during July, 1915. Each cyst is accompanied by a small amount of pigment in the more advanced stages, although I have seen many of them with no pigment and nearly the same appearance as the muscle (Fig. 7). One must often pick the muscle fibers apart in order to find the cyst as most of them do not show on the surface. I have not been able to discover that they are found in any definite region of the body, although they are more numerous near the dorsal fin.

A photomicrograph of a young cyst shows a number of blood vessels entering one end of the cyst. The cyst

itself contains numerous blood corpuscles, as if they had been emptied into the cyst. The difficulties of fixation have prevented me thus far from studying the character of the blood in these cysts.

As the cyst grows, the wall of which is made up of connective tissue, partitions are formed which grow in from the main outside wall. The result is that in the older stages three to five separate cavities are found in each cyst (Fig. 6), although but a single larval Trematode is present in each cyst. I have opened a large number of these cysts and thus far have found no exceptions.

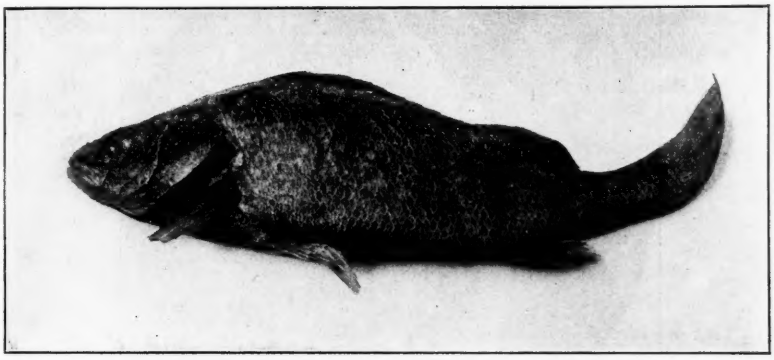


FIG. 5. The perch (*Perca flavescens*) showing minute distomes embedded in the skin and fins. These parasites can be recognized in the photograph as minute, black spots. The black pigment surrounds the parasite.

Not much can be said at this time in regard to the structure and changes through which this larva is passing. That it is growing there can be no doubt, as different stages showing the presence or absence of some of the mature organs were found. In most of the whole larvæ dissected and mounted, the excretory ducts are completely formed, while the digestive tract is limited chiefly to the anterior end. Two suckers can be recognized and a part of the reproductive organs. The whole animal is so very small that it can scarcely be seen with the unaided eye. It will require better fixation before the species can be determined accurately. I am inclined to

believe that it is the larval stage of either some species of *Holostomum* or *Clinostomum*. The latter is more numerous in this lake; but the size and pigment strongly suggest *Holostomum*, the adult appearance of which is shown in the photomicrograph (Fig. 7).

From the studies thus far made, I am inclined to think that it takes one season for this larva to transform into the adult worm. My reason for this conclusion is that

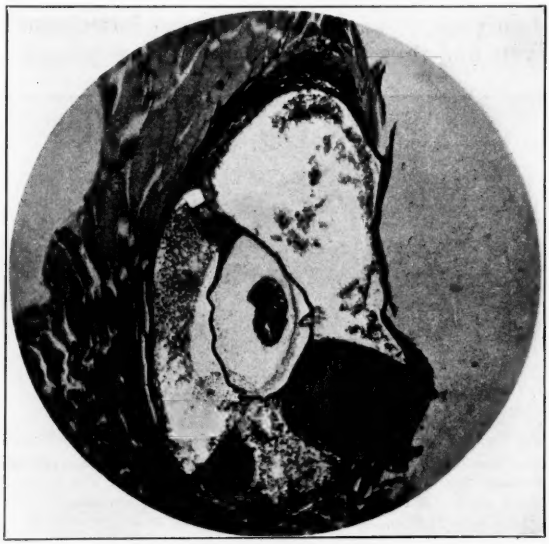


FIG. 6. Photomicrograph of the larval cyst of an undetermined distome. Each cyst contains but a single young worm, although there are several partitions. The cyst is surrounded by several layers of connective tissue and is embedded in the muscles.

there is so little difference between the several stages that I have secured.

In the hope of throwing some light upon the relation of Trematodes to fish, the writer urged several years ago that some "grubby" perch be placed in a separate tank in one of the hatcheries and fed for one year to see what happened, but the suggestion was rejected as not practical, although a number of specific experiments were out-

lined. It is unnecessary to say that many thousands of dollars' worth of fish would be rendered available throughout the United States, if this one disease alone could be prevented. Perch and bass which are so generally infected with Trematodes are delicious pan fish and usually easily caught in large numbers. It would seem as if the mere calling attention to this large amount of food annually wasted would stimulate some organization to finance the necessary scientific investigation. Such an investigation would need to continue at least two years and possibly longer; but the expense involved would be a small fraction of the returns, if the disease could be prevented.

"Grubby" perch are but one illustration of the diseases that occur in our fresh-water fish. There are a number of diseases due to bacteria and others caused by certain Soporozoa, Fig. 7. These diseases are usually epidemic,

FIG. 7. *Leuciscus carletoni* (Kendall), black-stripped minnow. Taken in Lake Clear, 1916. Infected with *Myxobolus*, a sporozoan parasite.

killing large numbers of fish in a few weeks. The main fact that is known now is that the fish die and several specific microorganisms are observed to be associated with certain ulcers, cysts, etc. But as to what causes lead up to the fatal termination of the diseases, little is known.

An admirable monograph upon carcinoma of the thyroid in the Salmonoid fishes was prepared, but left incompleted because of lack of funds. This is about the only serious study of fish diseases that has been made in the United States.

At this time, when all are anxious to help in whatever way that they can, it may be permissible to suggest that

scientists may render real service along the general lines indicated in this paper. To be more specific, they may be summarized as follows:

1. A critical study of the life of the fresh-water ponds and streams is very desirable.

(*a*) To determine the life history and food habits of the small fish and invertebrates present.

(*b*) To determine the amount and conditions of plant life—the ultimate source of food for all animals.

(*c*) To determine if more plants can be made to grow in water naturally lacking sufficient plant life.

(*d*) To determine if it is possible to introduce enough natural food for fry and fingerlings to keep them from starving, as many of them probably do now in such ponds as many of those in the Adirondacks.

(*e*) To determine to what extent the natural food of the fish is eaten by invertebrates living in the same waters.

When these problems are solved, the next step in efficiency in fish culture can be taken. It will require the cooperation of many scientists. The result will be the substitution of an intelligent method of restocking in place of the present one, which is often unintelligent or politically influenced.

2. A detailed study of the several diseases occurring in fish.

(*a*) It is necessary to know the complete life history of such parasites as the Trematodes before any one can formulate preventive measures. There are at present at least four different species of Trematodes found in our fresh-water fish and the complicated life history of each is unknown.

(*b*) The causes leading up to the usual epidemics in fish must be determined before these can be prevented. This is a problem for the bacteriologist and the protozoologist.

When these problems are worked out, an enormous amount of fish food will be conserved for human needs.

SYRACUSE UNIVERSITY,
October 29, 1917

BIBLIOGRAPHY

The following list of references includes only those works cited in the preceding pages. A more extended reference to the literature will be found in F. C. Baker's paper, which is the first one given in the list below.

Baker, Frank Collins.
1916. The Relation of Mollusks to Fish in Oneida Lake. Technical Publication No. 4. The New York State College of Forestry at Syracuse University, pp. 1–366.

Bean, Tarleton H.
1903. Catalogue of the Fishes of New York. Bull. No. 60. New York State Museum, pp. 1–784.

Calkins, Gary N.
1899. Report upon the Recent Epidemic among Brook Trout (*Salvelinus fontinalis*) on Long Island. Fourth Annual Report of the Commissioners of the Fisheries, Game and Forests of the State of New York. Report for the year 1898, pp. 175–189.

Colbert, Roy J.
1915. An Ecological Study of the Fish of the Douglas Lake Region, Michigan, with special reference to the mortality of the species. Michigan Geological and Biological Survey. Publication No. 20, Biology Series No. 4, pp. 25–57.
1911–12. The Brook Trout Disease in Wisconsin Waters. Report of the Wisconsin Commission of Fisheries, pp. 11–21.
1913. The Behavior of a Parasitic Copepod. *Jour. Animal Behavior*, Vol. 8, pp. 36–60.
1914. Fertilization in the Parasitic Copepod, *Lernæopoda edwardsii*. *Biol. Bull.*, Vol. 27, pp. 115–121.

Fenneman, N. M.
1910. Lakes of Southeastern Wisconsin. Published by the State of Wisconsin.

Forbes, Stephen A.
1883. The First Food of the Common Whitefish (*Gorogonus clupeiformis* Mitchill). Bull. Ill. State Lab. Nat. Hist., I, No. 3, pp. 95–110.

Gaylord, H. R., and Marsh, M. C.
1912. Carcinoma of the Thyroid in the Salmonoid Fishes. Bull. Bur. Fisheries, Vol. XXXII, 1912. Document No. 790. Issued April 22, 1914.

Gurley, R. R.
1894. The Myosporidia or Psorosperms of Fishes, and the Epidemics Produced by Them. U. S. Commission of Fish and Fisheries. Commissioners' Report, 1892, Published 1894. Pp. 65–359.

Hankinson, Thomas L.
1914. Young Whitefish in Lake Superior. *Science*, N. S., Vol. 40, No. 1024, p. 239.
1915. Observations on the Fishes of Houghton County, Michigan. Michigan Geological and Biological Survey. Publication No. 20, Biological Series No. 4, pp. 11–22.

Needham, J. C., and others.
1903. Aquatic Insects in New York State. Bull. 68. New York State Museum.

Needham, J. C., and others.
1905. May Flies and Midges. Bull. 86. New York State Museum.

Reighard, Paul.
1908. A Plan of Promoting the Whitefish Productions of the Great Lakes. Bull. U. S. Bureau of Fisheries, XXVII, pp. 643–84.
Smallwood, W. M.
1914. Preliminary Report on Diseases of Fish in the Adirondacks. A Contribution to the Life History of *Clinostomum marginatum*. Technical Publication No. 1. The New York State College of Forestry at Syracuse University, pp. 1–27.
Smith, Henry I.
1874. The Crustacean Parasites of the Fresh-water Fishes of the United States. U. S. Fish Commission. Report for 1872–73.
Wilson, Charles B.
1915. North American Parasitic Copepods Belonging to the Lernæopoda, with a revision of the entire family. No. 2063. Proceedings U. S. National Museum, Vol. 47, pp. 565–729.

SHORTER ARTICLES AND DISCUSSION

MODIFICATIONS OF THE 9:3:3:1 RATIO

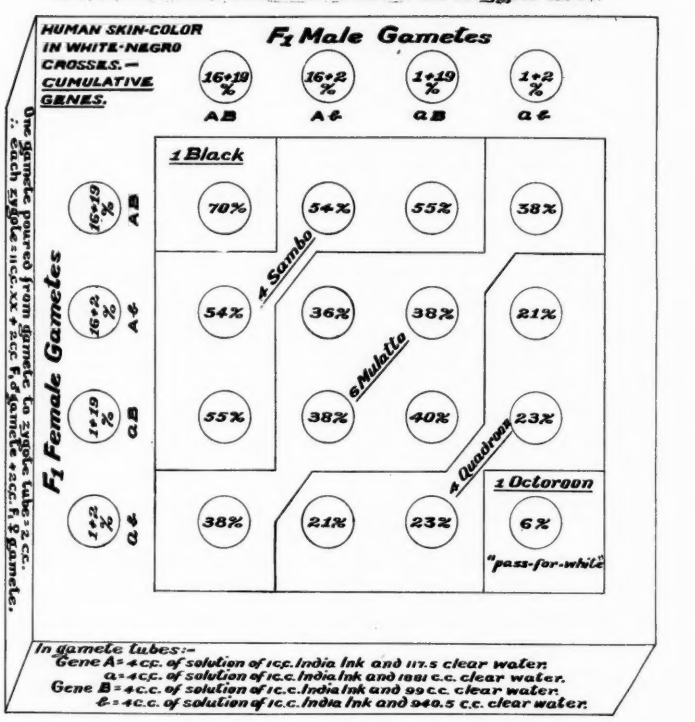
A. Chemical Experiments Paralleling the Several Possible Modifications of the Mendelian F_2 Di-hybrid Phenotypic Non-blending Ratio 9:3:3:1

The foundation F_2 di-hybrid ratio 9:3:3:1 consists of 9 individuals having somatic traits both "A" and "B," 3 individuals having "A" only, 3 having "B" only, and 1 having neither "A" nor "B." Or, if each allelomorphic pair consists, not in a gene and its absence, but in genic entities contrasted in quality or quantity and showing clean-cut dominance and recessiveness, in 9 "A" and "B" both dominant; 3 "A" dominant, "b" recessive; 3 "a" recessive, "B" dominant; 1 "a" and "b" both recessive. This di-hybrid ratio was one of the early discoveries of Mendel[1] himself, but after the revival of genetical studies in 1900 experimental breeding had not continued long before modifications of this ratio became apparent. Thus Bateson[2] mentions a number of cases in which the 9:3:4 F_2 ratio is found. It is apparent in such cases that two unit trait-pairs are involved, that the dominant phase of one of them standing without that of the other in 3 individual F_2 somas is not to all patent aspects different from the 1 individual possessing the dominant phase of neither of the two trait-pairs involved. In the gametes of individuals of families that produce the 9:3:4 ratio the segregation and recombination of genes are, however, just as clean-cut and follow the same rule as in pedigrees giving the unmodified foundation ratio 9:3:3:1; only the somatic working out of the genes is different in the two ratios.

Barring blending, linkage, crossing-over, non-disjunction, sex-limited inheritance and other special phenomena, which limitations preserve intact the numerical entities 9, 3, 3, and 1, the

[1] Mendel, G., "Experiments in Plant Hybridization" (reprinted in English in Bateson's "Mendel's Principles of Heredity," pp. 334–379), p. 351, 1866.

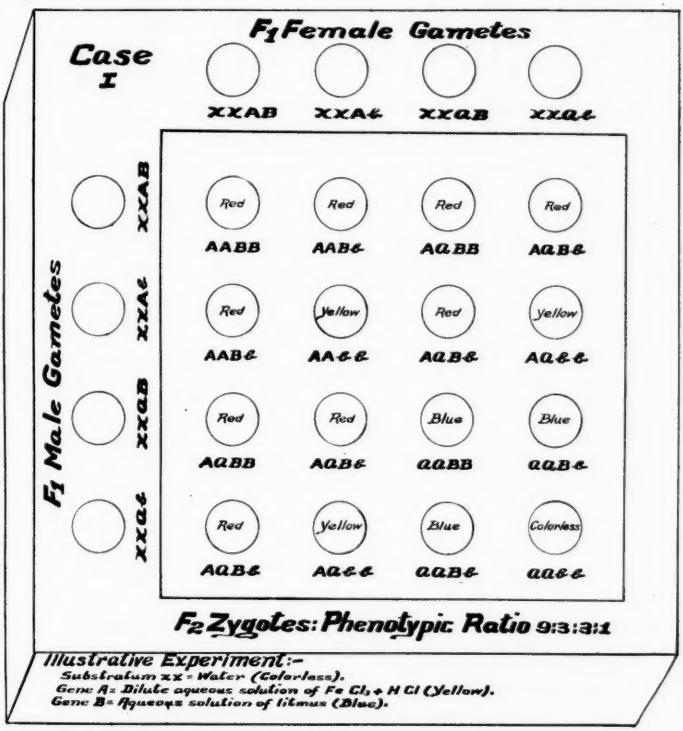
[2] Bateson, W., "Mendel's Principles of Heredity," p. 80, 1913.


Experiment Illustrative of Black Skin-Pigment Inheritance:-
Substratum xx = 11 cc. clear water in each of the 16 zygote tubes.
HUMAN SKIN-COLOR IN WHITE-NEGRO CROSSES.— CUMULATIVE GENES.
F1 Male Gametes
16+19 % AB
16+2 % Ab
1+19 % aB
1+2 % ab
F1 Female Gametes
One gamete poured from gamete to zygote tube = 2 cc.
∴ each zygote = 11 cc. xx + 2 cc. F1 ♂ gamete + 2 cc. F1 ♀ gamete.
1 Black
70%
54%
55%
38%
4 Sambo
54%
36%
38%
21%
6 Mulatto
55%
38%
40%
23%
4 Quadroon
38%
21%
23%
6%
1 Octoroon
"pass-for-white"
In gamete tubes:-
Gene A = 4 c.c. of solution of 1 c.c. India Ink and 117.5 clear water.
a = 4 c.c. of solution of 1 c.c. India Ink and 1881 c.c. clear water.
Gene B = 4 c.c. of solution of 1 c.c. India Ink and 99 c.c. clear water.
b = 4 c.c. of solution of 1 c.c. India Ink and 940.5 c.c. clear water.

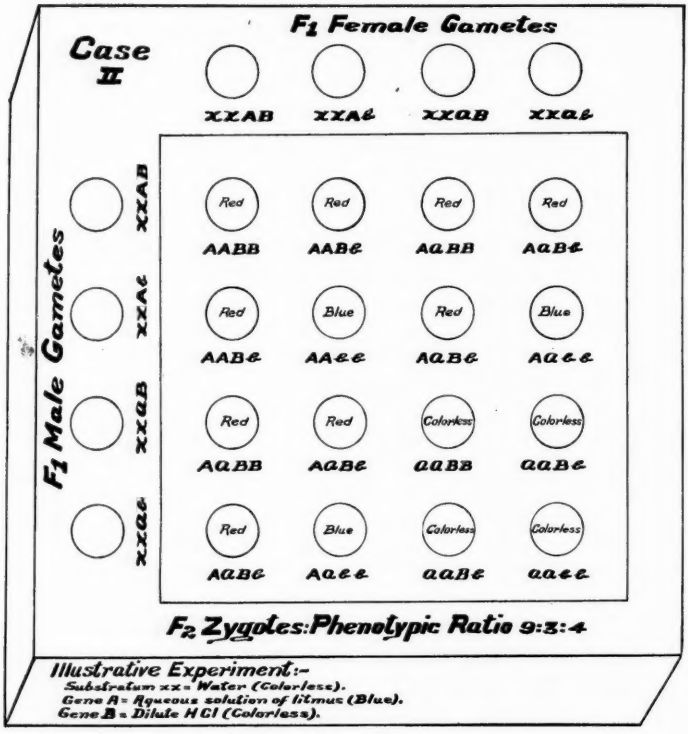
following table presents in orderly fashion all of their possible ratio-recombinations:

Series A

Case	I.	9:3:3:1.
Case	II.	9:3:4.
Case	III.	9:6:1.
Case	IV.	9:7.
Case	V.	10:3:3.
Case	VI.	10:6.
Case	VII.	12:3:1.
Case	VIII.	12:4.
Case	IX.	13:3.
Case	X.	15:1.

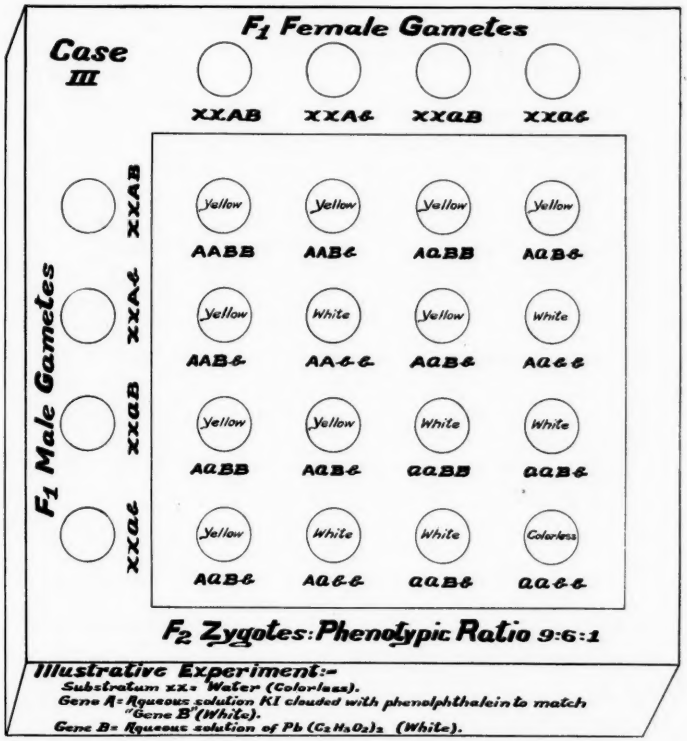


The chemical experiments described in the accompanying figures parallel chemically what must happen to the F_1 genes in their development into traits in the F_2 somas in each case of a modified somatic di-hybrid ratio. Each drawing represents a 2-inch wooden block $7\frac{1}{2}$ inches square, with twenty-four $\frac{5}{8}$-inch holes, $1\frac{1}{4}$ inches deep, suitable for holding test-tubes. The four holes at the top hold test-tubes containing chemicals representing the four types of F_1 female gametes possible when di-hybridism is being considered; the four to the left perform the same service for the four male gametes. The sixteen holes blocked off in the square hold test-tubes for the sixteen types of zygotes resulting, by the checker-board method, from all possible unions of the four male and the four female gametes. X X represent the substratum or the sum-total of hereditary qualities other than the traits under consideration. The lettering under each test-tube circle is the genetic formula for the gamete, or zygote as the



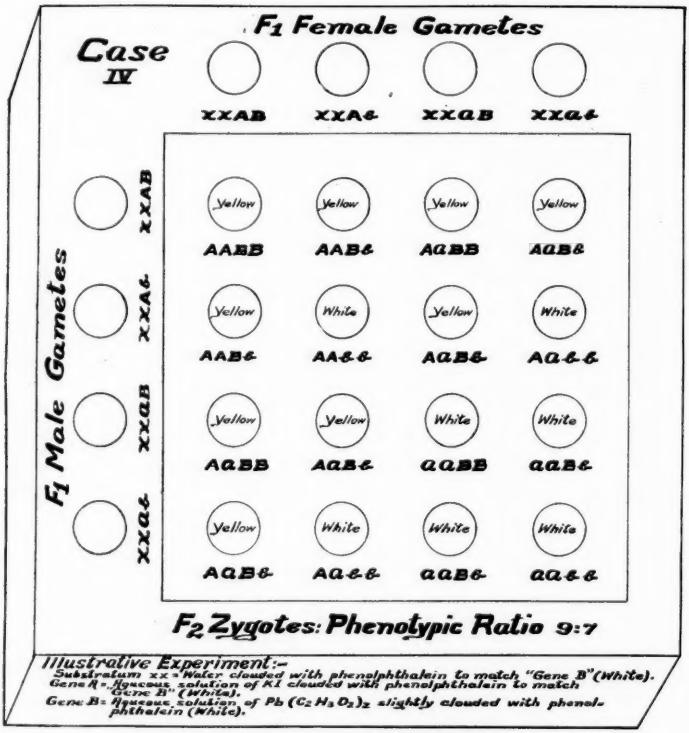
case may be. A word within a test-tube circle names the color of the reaction-product, which color is the index or analog of the somatic working out of its accompanying genetic formula of the soma.

Instructions for performing the experiment illustrative of each ratio-modification are found in detail in the drawing for the selected case. The chemicals representing gene "A" and gene "B" and the substratum are, as indicated, poured into the test-tubes representing the F_1 female and the F_1 male gametes. Each gamete-holding test-tube should contain approximately 20 c.c. of the appropriate genes and substratum. Of this mixture 4 c.c. represent 1 gamete; and 1 such gamete is to be poured into each one of the 4 zygote-holding test-tubes, directly below or directly to the right, as the case may be, of particular gamete-holding test-tube, following the checker-board method. Thus each of the 16 zygote test-tubes will contain chemicals appro-



priately representing 1 F_1 male and 1 F_1 female gamete free, like the constituents of a united sperm and egg, to interact in the zygote and in subsequent ontogenesis.

Some of these ratios, such as exist in Cases Nos. V, VI and IX, are much more difficult chemically to contrive than others, such as Nos. I, II, III, IV and X. It is not surprising, then, that nature provides more readily cases in inheritance representing the latter ratios, while the former are being found only by the most diligent genetical study. Not all of these ratios have yet been found in nature by experimental breeding, but, from time to time, a geneticist reports the discovery of a new di-hybrid F_2 ratio which proves to be a member of this series. Doubtless all of them will be found in time, but without introducing the special phenomena earlier referred to, Series A, consisting of 10 cases, exhausts the possibilities of F_2 phenotypic di-hybrid ratios.

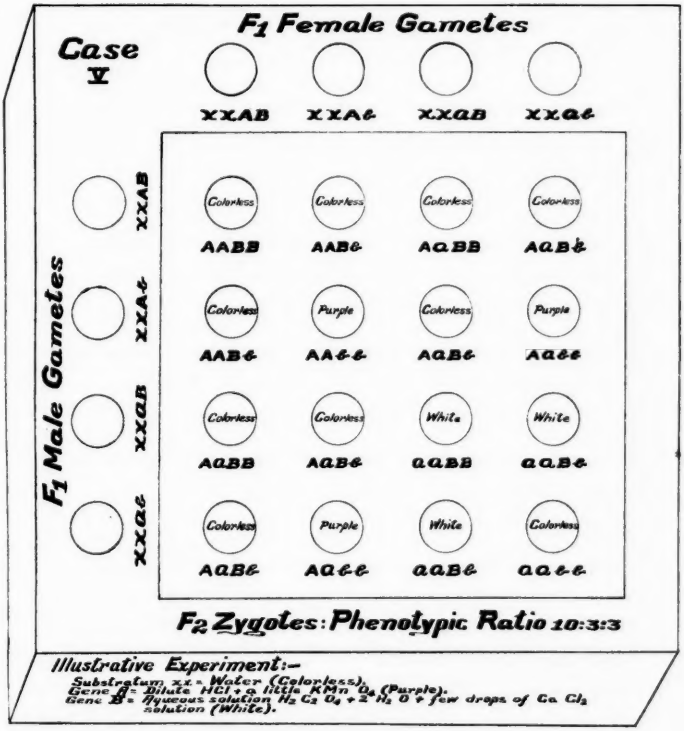


B. A CHEMICAL EXPERIMENT PARALLELING A MODIFICATION OF THE MENDELIAN F_2 DI-HYBRID PHENOTYPIC RATIO 1:2:1:-2:4:2:1:2:1 INVOLVING SOMATIC BLENDING AND GENIC SEGREGATION IN THE F_1 GENERATION

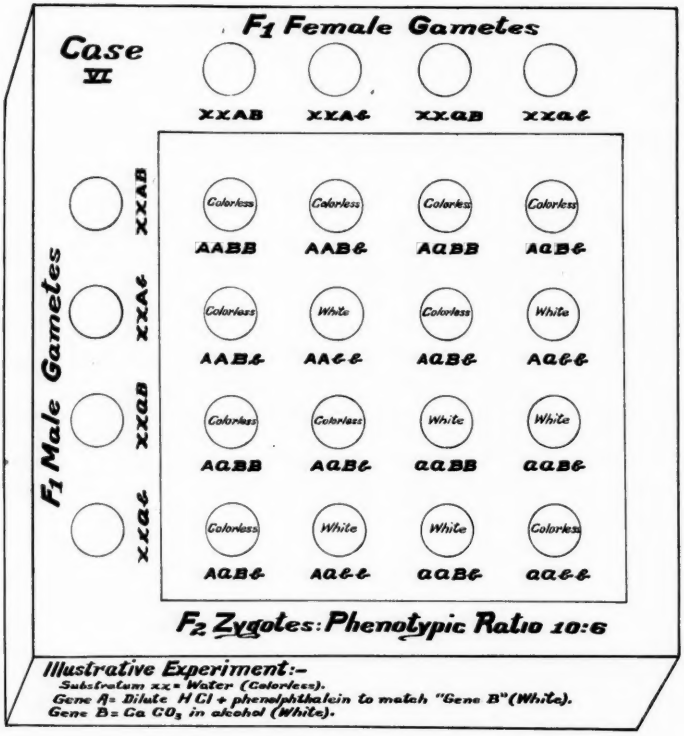
The ten cases described in the Series A are non-blending, in which the entities 9, 3, 3, and 1 are kept intact, that is, they are simply recombined. The mono-hybrid ratio on which they are based is the normal dominant-recessive 3:1 relation. The typical blending ratio in the F_2 mono-hybrid is 1:2:1. Carrying this latter ratio into the di-hybrid classification in the same manner as the 3:1 ratio was carried into the 9:3:3:1 classification gives us the following: 1:2:1:2:4:2:1:2:1, a total of sixteen individuals divided into 9 classes.

In Davenport's[3] study on the "Inheritance of Skin-Color in

[3] Davenport, C. B., "Skin-Color in Negro-White Crosses," Pub. 188 Car. Inst. Wash., 1913.

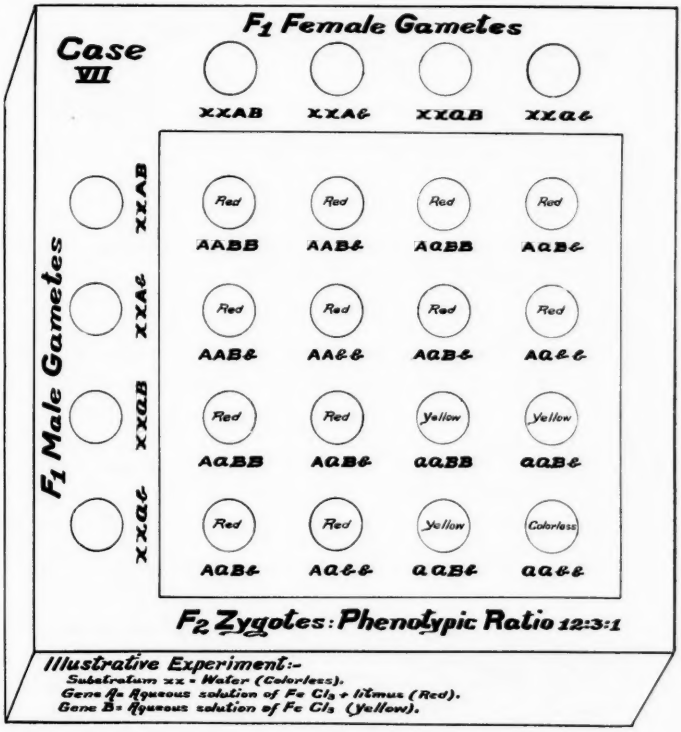


Negro-White Crosses'' he found that the amount of black skin-pigment in an individual is determined by two genes in each parental gamete, and in measuring the intensity of black skin-pigment in the members of a great many highly hybridized families he found 5 definite maxima in the curve plotting the distribution of individuals according to the per cent. of black skin-pigment carried. Theoretically (unless genes ''A'' and ''B'' are exactly equally potent in developing into a definite per cent. of blackness showing in the unweathered skin) there should have been 9 maxima in the above-described distribution curve. Arbitrarily giving the genes the following potentiality for somatic expression, ''A'' 16 per cent., ''B'' 19 per cent., ''a'' 1 per cent., ''b'' 2 per cent. (which is not far from the the facts of the case), the somatic frequencies and black skin-color percentages would run as follows: One 70 per cent., two 54 per cent., one 36 per cent., two 55 per cent., four 38 per cent.,



two 21 per cent., one 40 per cent., two 23 per cent., and one 6 per cent., in a total of 16 individuals.

But practically 5 instead of 9 somatic types were actually found because gene "A" and gene "B" are so nearly equal in value that it is not possible in a given individual, simply by measuring the skin-color pigment, to determine whether gene "A" or gene "B" is responsible for the quantity of melanin possessed. Thus in the 5 classes the two 54 per cent. cases (AABb) and the two 55 per cent. cases (AaBB) constitute the three quarters blacks or "sambos," the two 21 per cent. (Aabb) cases and the two 23 per cent. (aaBb) cases constitute the one quarter blacks or "quadroons," while the one 36 per cent. (AAbb) case and the one 40 per cent. (aaBB) case are so nearly like the four 38 per cent. (*i. e.*, the "mulatto" AaBb) that they constitute a single class of six individuals. Hence the contracted ratio 1:4:6:4:1.

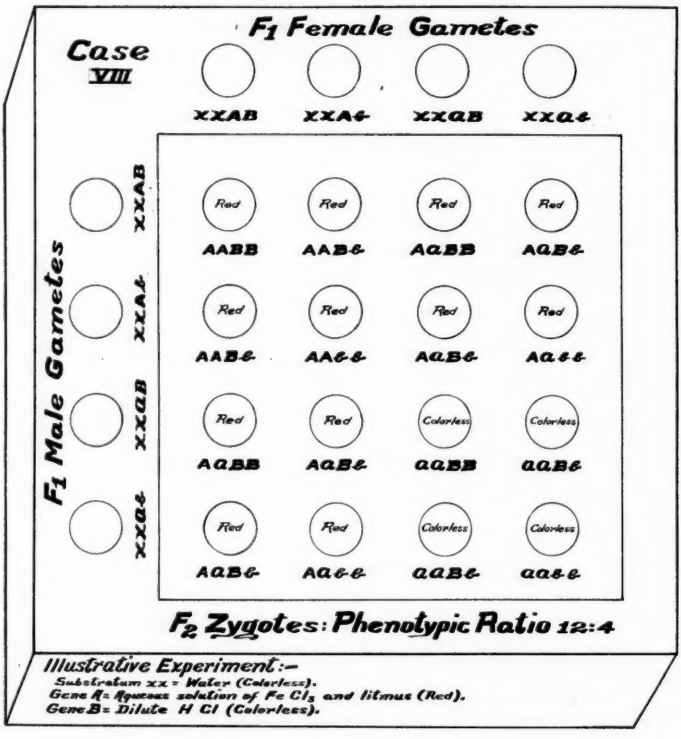


As Davenport clearly points out in the matter of black skin-pigment, each gene finds its definite somatic expression regardless of the presence of other genes. Since the two genes work out into the same somatic trait (*i.e.*, are duplicate genes) which somatic expressions differ only in quantity, they might well be be called cumulative genes. The accompanying diagram (Experiment Illustrative of Black Skin-Pigment Inheritance) gives specific directions for running this experiment in a manner very closely paralleling what Davenport found in nature.

This experiment illustrates only one case in a long possible series of modifications of the foundation F_2 di-hybrid phenotypic blending ratio 1:2:1:2:4:2:1:2:1.

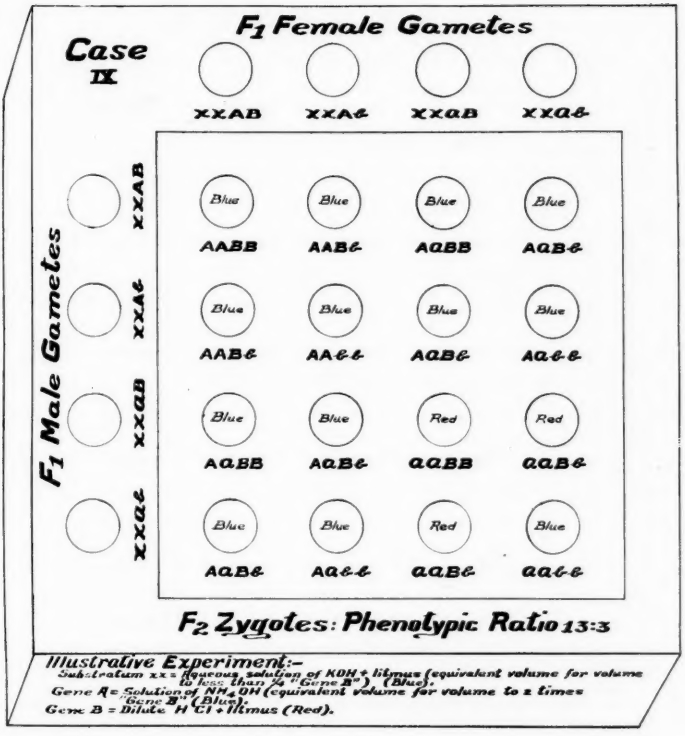
C. Other F_2 Di-Hybrid Series

In a case in which gene "A" does not blend with its allelomorphic mate "a" in the F_1 soma, but presents a typical case of

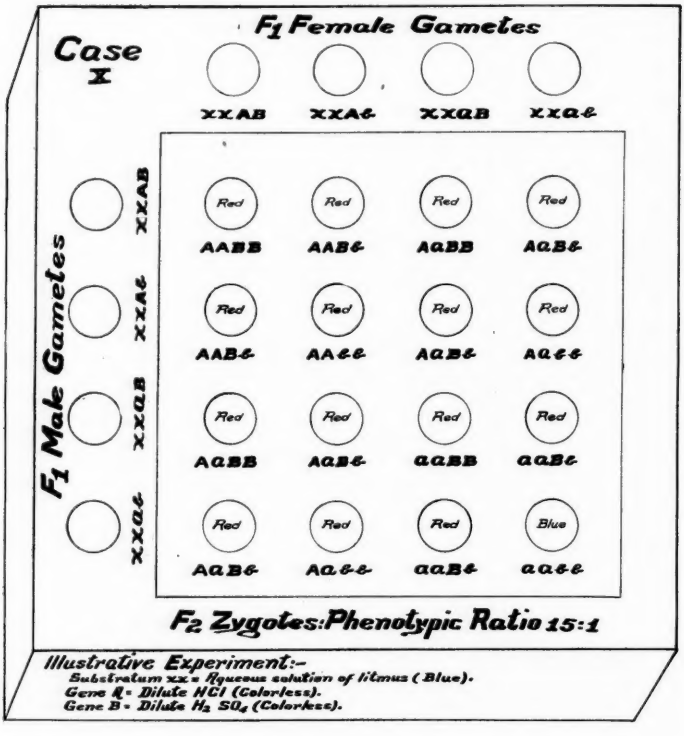


Mendelian dominance, while gene "B" blends with its mate "b" in the F_1 soma, the di-hybrid F_2 ratio resulting from combining two such trait-pairs is found by multiplying the F_2 mono-hybrid dominant relation $3+1$ by the F_2 mono-hybrid blending relation $1+2+1$, giving when expressed as a ratio the somatic F_2 di-hybrid relation $3:6:3:1:2:1$. Among other special cases to be considered are those involving crossing-over, non-disjunction and sex-limited inheritance.

When the genic and somatic specifications of a ratio are known it is not difficult to contrive a chemical parallel for it. The use of such experiments consists not only in clarifying the conception of the particular situation at hand, but also in providing in the laboratory a nearer approach than is usually used for demonstration to what is actually happening in heredity. The chemical analogy between what happens in the zygote-holding test-tube and what actually happens in the somatic working out of the



segregable genes in the members of the F_2 ratios is doubtless much closer than any completely mechanical contrivance can show. In the experiments the blending quite properly is shown complete in the zygote and soma, but if the analogy were carried still further one should be able to dip into the gamete-holding test-tubes and there find that some of the original F_1 genes remain unchanged—the unchanged germ-plasm which is left behind—and to lift out well-defined gametes with "A" or "a" and "B" or "b" variously combined, according to the constituent genes of the zygote, for in the living germ-cell cycle, not the blending of the soma, but clean-cut segregation is the rule. Representing the gametes by capsules containing genes in solid form, which capsules and genes would be slowly soluble in the substratum of the zygote, would drive the analogy a little closer to nature.



REFERENCES

Johannsen, W. Elements der Exakten Erblichkeitslehre, pp. 526–8, 1913.

Laughlin, H. H. The F_1 Blend Accompanied by Genic Purity. AMER. NAT., pp. 741–751, 1915.

Shull, G. H. A Simple Chemical Device to Illustrate Mendelian Inheritance. *Plant World*, Vol. 12, pp. 145–153, 1909.

COLD SPRING HARBOR H. H. LAUGHLIN.

THE FACTORS FOR YELLOW IN MICE AND NOTCH IN DROSOPHILA

IN a recent number of THE AMERICAN NATURALIST[1] appeared a paper by Ibsen and Steigleder on "Evidence for the Death in Utero of the Homozygous Yellow Mouse." In summing up (p. 751), after stating that "our evidence tends to confirm the conclusion of Castle and Little that in mice homozygous yellow zygotes are produced in the yellow × yellow mating, but that these

[1] Vol. LI, No. 612, December, 1917, pp. 740–752.

zygotes fail to develop normally after implantation in the uterus,'' they suggest ''that in mice there may be a 'lethal factor,' similar to those so well known in *Drosophila*, which is so closely linked to the factor for yellow that they are practically at the same locus and there is consequently no crossing-over.''

If the postulated factors are indeed so closely linked that crossing-over *never* occurs, would it not be simpler and even more logical to assume that but a single allelomorphic pair of factors is involved? Such an assumption necessitates a second, namely, that one of the factors of this pair is dominant in one of its expressions (yellow) and recessive in a second (lethal).

Morgan[2] has recently made a similar assumption for the mutant sex-linked factor in *Drosophila* which causes ''notch'' in the wings. He states that it is ''dominant in regard to the wing character but recessive in its lethal effect. A female with notch wings carries the gene in one of her X-chromosomes and the normal allelomorph in the other X-chromosome. Half of her sons get the former and die, the other half get the latter X-chromosome and live. As there are no lethal bearing males, the females must in every generation be bred to normal males.''

If Morgan is right in his assumption, there seems to be no reason, *a priori*, why factors having both dominant and recessive expressions should be limited to sex-chromosomes.

Stating that crossing-over has not been observed in a certain number of generations, even though the number of both individuals and generations is large, is, however, a very different matter from proving that crossing-over *never* occurs. Just where the evidence ceases to be negative and becomes positive, perhaps depends upon the ratio between the space occupied by a factor and the total length of the chromosome bearing it, in its relation to the law of probability, and to possible factors restricting crossing-over.

The data necessary for such a calculation does not appear to be available for either mice or *Drosophila*. Which interpretation is assumed must therefore for the present be a matter of personal preference. The continued failure to find crossing-over will in each case tend to make the one involving a single allelomorphic pair of factors more probable.

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January, 1918

[2] AMER. NAT., Vol. LI, No. 609, September, 1917, pp. 513–544.

NOTES AND LITERATURE

Genetics in Relation to Agriculture. By E. B. Babcock and R. E. Clausen. New York: McGraw-Hill, 1918. Pp. ix–xx + 675, Fig. 239, Pl. 4.

Every geneticist who opens this volume in a spirit of hope and expectation will close it with appreciation and satisfaction, with a feeling that a tremendous task has been worthily accomplished. Unquestionably it will fill a real need as a text-book. In addition it should be of great service to the general biologist —using that term in its broadest sense—who wishes to have a compendium of genetical facts for ready reference.

The work is divided into three parts; it is really three volumes in one. In the first part the fundamental principles of genetics are outlined, in the second plant breeding is discussed, in the third animal breeding is considered.

There are thirty-nine chapters and an excellent glossary. The bibliography of twenty-four pages is not complete and does not purport to be complete. It is a list of the actual titles consulted in the preparation of the manuscript, truly no light undertaking.

The reputation of both authors as careful investigators is so firmly established that one is not surprised to find the immense volume of genetic literature of the past eighteeen years judiciously weighed and sifted, but that they found the time during the selection of material for so much constructive and illuminating criticism is perhaps not to have been anticipated. Moreover, since an investigator is not necessarily a good text-book writer, one suspects that the general excellence of the book from the pedagogical standpoint is due largely to Dr. Babcock's special training and long experience as a teacher.

After an introductory chapter on the methods and scope of genetics, the authors have chosen to open the volume by treating variation. Several modifications of older classifications of variation are given which may or may not prove useful. They were probably included rather tentatively as introductory to the main business of the chapter, the action of external stimuli in modifying development and causing germinal variation. Some of the illustrations here are not all that might be desired,

for example, the work of T. H. White on making new varieties of tomatoes by adding large quantities of fertilizers, which is rather hesitatingly cited. But perhaps one should criticize matter which does not appear rather than matter which does appear. In other words, if the reviewer may express his own hope in the connection, it is to see a more extended, well-rounded discussion of the action of the factors of environment in a later addition.

The statistical study of variation has been given a very pleasing treatment. The mathematician will undoubtedly complain that it is amateurish because it is given with a minimum of technical language. But just there lies its value in such a text-book. The necessary statistical tools are described so clearly that the elementary student can hardly err in their use. The more advanced student is properly directed elsewhere.

The physical basis of heredity is also discussed with great independence. The chromosome hypothesis is accepted without reservation. Cytological details not bearing directly on the subject in hand are not even mentioned, while those described—though accurate as far as they go—are somewhat diagrammatic. It will be interesting to see how this treatment works out in the classroom. No doubt many will find it a welcome change from the interminable details of unknown significance that often fill the pages of books on genetics. At the same time it is perhaps to be regretted that the difference between the higher plants and the higher animals in gametogenesis, and the bearing on genetics of the conflict between supporters of parasynapsis and telesynapsis, are not given more space.

A hundred and fifty pages are devoted to Mendelian interpretations of breeding facts. A wealth of illustration is used, and almost all types of Mendelian ratios are represented, although it is not easy to gather them together in a general *ensemble*. The older treatments of Plate and of Goldschmidt, where every theoretical modification of the Mendelian ratio was mentioned and then a case in point cited, had their value from a pedagogical standpoint, and it is rather to be deplored that their use was not continued. The newer data, in particular the work of Morgan and his students, is admirably presented, however. For the first time text-book treatment of crossing over, interference, and the various other phenomena discovered in *Drosophila,* is given in such a manner that the beginning student should be able to grasp the essential points without difficulty.

Interesting chapters on species hybridization, pure lines and

mutations comprise the remainder of part one. The discussion of mutations will probably not please DeVries, but it certainly is more in accord with all the facts than most other essays on the subject.

The applied genetics, animal breeding and plant breeding, filling twenty-four chapters, ought to be received with great approbation. Its compilation must have been very difficult, and its usefulness should be in direct proportion to the work involved. There is a great deal of new material of a strictly practical nature such as the origin of sweet pea varieties, breeding disease-resistant plants, etc. On the other hand, there is really no definite line to be drawn between part one and parts two and three. Theoretical genetics runs all through the book. For example one finds the treatment of heterosis, graft-hybrid chimeras and bud mutations in part two; and in part three discussions of Mendelian inheritance in domestic animals, acquired characters, non-Mendelian theories of sex-determination, the hormone theory, etc. The work is so well done that it must be read to be appreciated. The reviewer has but one suggestion to make concerning it, and this not in the nature of a criticism. Partially sterile hybrids between species, as is shown in Chapter 12, supply particularly useful material for the improvement of domestic animals and cultivated plants. If one studies carefully the history of domestic species, fragmentary as it is, he is astounded at the enormous number of cases in which the ancestry involves two or more species. Would it not be well to emphasize this point by extended illustrations in a book on plant and animal breeding?

The authors are to be congratulated on having brought together the material for a classical text-book on genetics. Revision will doubtless soon be necessary as is suggested in the preface. If it is made with the care that such an excellent foundation deserves the work will unquestionably go through many editions.

The McGraw-Hill Company deserve no little credit for the generous way in which they have seconded the authors' efforts. The typography, illustrations, paper and binding are extremely good. We understand that this is their first contribution toward a series of agricultural text-books under the general editorship of C. V. Piper. A standard has been set that is a good augury for the future.

E. M. E.